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ENETICS

# of YELLOW BIRCH

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Clausen, Knud E.

1973. Genetics of yellow birch. USDA For. Serv. Res. Pap. WO-18, 28 p.

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This publication is one in a series on the genetics of important forest trees of North America being published by the Forest Service, U.S. Department of Agriculture, in cooperation with the Society of American Foresters. Development of this series is in accord with the resolutions of the World Consultation on Forest Genetics and Tree Improvement at Stockholm in 1963 and the Second World Consultation on Forest Tree Breeding at Washington, D.C., in 1969. The Committee on Forest Tree Improvement of the Society of American Foresters undertook the preparation of manuscripts for North American species.

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SUMMARY

Yellow birch is a valuable hardwood species with considerable potential for genetic improvement. This publication reviews current genetic knowledge and suggests means of utilizing it in tree improvement programs.

Taxonomic problems concerning *Betula alleghaniensis* Britt. are reviewed and the evolution, migrational history, and distribution of the species as currently understood are discussed.

The phenology of male and female inflorescence development, pollen release, and seed maturation and dispersal in yellow birch is summarized. The species begins to flower at age 15 to 20 but has the potential for earlier prolific seed production. Yellow birch exhibits a moderate degree of self-compatibility and some intraspecific incompatibility; it crosses naturally with several other species. Techniques for pollen extraction and storage, controlled pollination, and methods of establishing experimental material in the nursery and field are described.

Yellow birch can be propagated readily by grafting and some suitable methods are outlined. Reliable techniques for rooting of cuttings are lacking.

The species shows considerable phenotypic variation in leaf, catkin, fruit, pollen, and bark characteristics. Variation has also been demonstrated in tree growth and quality characteristics and in the phenology of growth.

Provenances show considerable variation in hardiness, growth, concentration of wintergreen oil, and sensitivity to gamma radiation. The variation in most characteristics appears to be random and poorly related to the geographic origin of the provenances. Only initiation and cessation of growth show clinal variation patterns.

Genetic variation among individual trees appears to be much greater than provenance variation. Heritability estimates of juvenile height growth are fairly high, indicating that selection for height should be profitable. Seedlings with abnormal number, shape, and color of cotyledons have been observed at varying frequencies.

Interspecific hybridization attempts with yellow birch as female or male parent are summarized. Although yellow birch can be crossed artificially with several other species, only a few of the hybrids have been verified and none have so far shown any hybrid vigor.

The species is hexaploid with $2n = 84$, but some variation in chromosome number appears to exist.

Yellow birch breeding programs should focus on improving tree quality and growth rate. The following options open to tree breeders are discussed: (1) selection of superior trees, (2) selection of superior provenances, (3) hybridization of superior individuals selected within provenance tests or progeny evaluations, (4) provenance hybridization, (5) species hybridization.

Gene pool reserves should be established in order to provide a reservoir of genetic diversity for future selection and breeding.

Studies of regional and local variation are needed. Multi-purpose testing of progenies is another high-priority field of research and components of growth require study. Research on seed orchard design and management is needed. Cytology and hybridization research are lower research priorities. Isoenzyme variation and other basic problems need study.

GENETICS OF YELLOW BIRCH

by Knud E. Clausen[1]

INTRODUCTION

Yellow birch (*Betula alleghaniensis* Britt.), one of the largest deciduous trees in northeastern North America, is in high demand for sawtimber and veneer. To ensure a steady supply of high-quality logs in the future, genetically improved planting stock must be developed and used.

Although some breeding work with birch species was done in the United States as early as 1940, most studies of yellow birch genetics have been carried out during the last 10 years. Research has shown that it is a variable species with considerable potential for genetic improvement.

The purpose of this publication is to review the current status of our knowledge, to point out areas in need of further research, and to suggest directions for developmental tree improvement programs.

TAXONOMY AND EVOLUTION

Yellow birch was originally described and named *Betula lutea* Michx. f. by Michaux (1812); most botanical handbooks continue to use this name (Rehder 1940, Fernald 1950, Gleason 1968). Little (1953), however, showed that the correct name for this species is *B. alleghaniensis* Britt.

Fernald (1922) distinguished trees with 8 to 13 mm. long fruiting bracts as var. *macrolepis* Fern., which is supposed to be more common in the northwestern part of the species range (Rehder 1940, Fernald 1950, Gleason 1968). It was recently transferred to the proper species name by Brayshaw (1966). Studies of natural variation in fruiting characteristics, however, cast doubt on the validity of this distinction. In a range-wide study of variation in yellow birch (Clausen 1968a), 55 percent of the 610 trees sampled had bracts 8 mm. or longer. Similarly, Dancik and Barnes (1972) reported an average bract length of 9 mm. for 66 trees in southeastern Michigan, and Sharik and Barnes (1971) found that bracts averaged 8.4 mm. in 19 F_1 trees originating from northwestern Massachusetts parents. Long bracts were also typical of 29 Appalachian birch populations studied by Sharik.[2] These stands had an average bract length of 9.4 mm. Thus, trees with long bracts are well distributed over the natural range of the species. They probably represent one extreme of bract-length variation. These trees have no other distinguishing characteristics and are not restricted geographically; thus, they should not be considered a separate variety.

Another variant, first described by Fassett (1932) from southern Wisconsin, is distinguished by its tight or only slightly exfoliating, dark gray to brown or black bark, which closely simulates that of sweet birch (*B. lenta* L.). It was named *B. lutea* forma *fallax* Fassett, meaning false or deceptive, because it had been misidentified as *B. lenta* and thus gave rise to erroneous reports of this species occurring in Wisconsin. Undoubtedly, failure to recognize this form of yellow birch also accounts for old records of *B. lenta* in southern Minnesota, southern Michigan, and northern Indiana (Dancik 1969), as well as unverified reports of its occurrence in southern Quebec and Ontario (Brayshaw 1966).

Forma *fallax* is now known from three counties in southern Wisconsin (Fassett 1932, Johnson[3]), one locality in central Wisconsin (personal observation), four counties in southern Michigan (Dancik 1969) and several localities in northern Indiana (Deam 1953) and northeastern Ohio (Braun 1961). Brayshaw (1966), in transferring this variant from *B. lutea* to *B. alleghaniensis*, also raised it from a form to the higher rank of variety. Dancik (1969) suggests that trees having these bark characteristics may be influenced by local environment and by genetic isolation. The uncertainty as to the genetic control of bark characteristics coupled with the scattered occurrence of this morphologically distinct variant strongly suggests that it does not deserve varietal rank but should be called *B. alleghaniensis* forma *fallax*.

The systematics of the genus *Betula* has been a subject of controversy and confusion for many years. Various classification schemes have been proposed; the one by Winkler (1904), followed in this publication, is outlined below.

- Section *Betulaster* (Spach) Regel
    - Subsection *Acuminatae* Regel
- Section *Eubetula* Regel
    - Subsection *Costatae* Regel
    - Subsection *Albae* Regel
    - Subsection *Nanae* Regel

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[2] Sharik, T. Oberlin College, Oberlin, Ohio. Personal communication, October 1971.

[3] Johnson, A. G. University of Minnesota, St. Paul, Minnesota. Personal communication, March 1971.

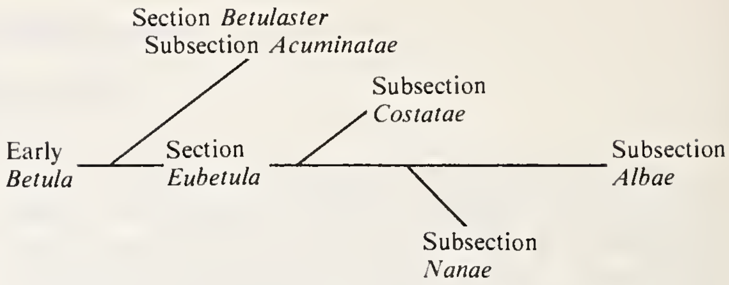
Approximately 52 species of *Betula* are currently recognized. Of these, members of the subsection *Acuminatae* are restricted to Asia. Subsection *Costatae*, on the other hand, occurs in both Asia and eastern North America, while subsections *Albae* and *Nanae* are widely distributed in Europe, Asia, and North America (Winkler 1904). One-half of the species occur in northeastern Asia and at least 18 species are native to China—a region containing one of the richest temperate zone floras in the world (Jung 1960). This would indicate that China, or at least northeastern Asia, may be the center of origin for the genus *Betula*.

Although about 135 extinct species of birch are known, the age of the genus remains uncertain. The earliest species belonging to the modern genus *Betula* date back to the Upper Cretaceous, but the genus apparently reached its greatest development during the Tertiary period (Berry 1923). Birches were very common in the Eocene and penetrated to Spitzbergen, Iceland, Greenland, and Alaska during the northward expansion of temperate forests. Fewer species are known from the Oligocene, whereas the birches were especially abundant during the Miocene (Berry 1923). The genus apparently declined somewhat during the Pliocene and was further reduced during the Pleistocene epoch of the Quaternary period.

Subsection *Acuminatae* is probably older than subsections *Costatae*, *Albae*, and *Nanae*. Members of *Acuminatae* occupy very restricted ranges in the Himalayas, southern China, and Japan. On the basis of flower and inflorescence characteristics (Abbe 1935) and wood anatomy (Hall 1952, Tabata 1964), *Acuminatae* appears to be the most advanced group. Tabata (1966) also found this group to be specialized ecologically. Considering the restricted ranges and habitats, and the specialized morphology and anatomy of these species, Tabata (1966) concluded that *Acuminatae* is the oldest group.

The *Costatae*, of which yellow birch is a member, also has somewhat restricted geographic ranges. Morphological characteristics of flowers, fruits (Abbe 1935), and wood (Hall 1952, Tabata 1964) in this group appear to be more advanced than those of the *Albae*. Most species of *Costatae* are restricted to certain habitats and are, therefore, ecologically specialized (Tabata 1966). *Costatae* thus appears to be the oldest group within section *Eubetula*. Although members of subsection *Nanae* have the most primitive wood characters (Hall 1952), they have somewhat specialized fruits and tend to occur in marshy or other specialized habitats (Tabata 1966). Species of *Albae* are widely distributed geographically and tend to be pioneer species. Morphologically they are primitive (Hall 1952, Tabata 1966). The lack of morphological and ecological specialization would indicate that *Albae* may be the most recent group of birches. A working hypothesis based on the above considerations is shown in next column.

Possible Infrageneric Phylogeny of *Betula*



Because little is known about evolution and migration of the genus in general, only subsection *Costatae* will be considered in the following. This group consists of at least 21 species of which 15 occur in northeastern Asia. Six species are still Chinese endemics, indicating that southwest China probably is the place of origin of the *Costatae*. From this center one species, *B. utilis* D. Don, has spread westward in the Himalayan Mountains to India and Nepal. A closely related species, *B. jacquemontiana* Spach, is only found in the western Himalayas (Kitamura 1964). Two species, *B. medwediewii* Regel and *B. raddeana* Trautv., have migrated as far west as northeastern Turkey (Acatay 1951) and the Caucasus and are completely isolated geographically from the main group of *Costatae*. Rehder's (1940) suggestion that *B. raddeana* may be related to *B. chinensis* Maxim. of northeastern China and northern Korea seems doubtful and has not been substantiated. From southwest China another group of species must have migrated northeastward. In addition to *B. chinensis* this group includes *B. costata* Trautv., which is now found in Korea, northeastern China, and the Maritime Region of Siberia and Sakhalin. Two species, *B. ermani* Cham. and *B. schmidtii* Reg., occur in the same general area but have also spread to Japan. Four species are currently found only in Japan.

The three North American *Costatae*, *B. alleghaniensis*, *B. lenta*, and *B. nigra* L., have migrated farthest from their presumed place of origin. A transatlantic or transarctic land connection between Europe and North America probably existed in the early Tertiary (Hopkins 1967), but the absence of fossil or living Costate birches in Europe makes it unlikely that the three *Costatae* reached North America from the east. More likely they migrated across the Bering land bridge during the Eocene when mixed mesophytic forests with *Betula* as a prominent component covered vast areas of northeastern Asia and Alaska (Wang 1961). Fossil leaves of a species identified as *B. sublutea* Tan. and Suz have been found at Cook Inlet, Alaska, in deposits considered to be of early or middle Miocene age (Wolfe *et al.* 1966). These forests encircled the North Pacific until the middle of the Miocene, but were replaced during late Miocene by boreal forests with different species composition in northeast Asia and in northwestern North America (Wolfe and Leopold 1967). Existing forests of China are considered lineal descendants of their Miocene counterparts (Wang 1961) and are much more similar to the forests of eastern North America than to those of Europe and Central Asia (Jung 1960). The *Costatae* could thus have reached eastern North America as early as the Eocene or as late as the middle of the Miocene. They probably became restricted to the East during the late Miocene or the Pliocene following the development of the plains in the central arid region of the continent (Berry 1923).

The relationship of *B. alleghaniensis* to other Costate birches is uncertain. Morphologically it is quite similar to *B. costata* of northeastern Asia, *B. grossa* Sieb. and Zucc. of Japan and to *B. lenta,* with which it is sympatric over most of the latter's range. These four species all have wintergreen oil in the inner bark of stems and branches (Rehder 1940, Anon. 1964); this chemical constituent is not known to occur in any other birches. This would indicate that these species are more closely related to each other than to the rest of the *Costatae.* Yellow birch has been crossed successfully with *B. lenta* (Woodworth 1931, Schreiner 1949, Clausen 1970b) and with *B. grossa.*[4] Both yellow birch and *B. grossa* are hexaploid species (2n = 84), while *B. lenta* is diploid (2n = 28) (Woodworth 1929). The chromosome number of *B. costata* is unknown.

The third American *Costatae,* the diploid *B. nigra,* is essentially incompatible with both *B. alleghaniensis* and *B. lenta* (Clausen 1970b) and thus appears only distantly related to these species. Rehder (1940), probably on the basis of similarity in fruiting bracts, considers *B. nigra* to be closely related to the Japanese *B. corylifolia* Regel, but it has apparently never been crossed with this species. *B. nigra* fruits mature in the spring, in contrast to those of all other birches. This is perhaps an adaptation to the flood plain habitat of the species, certainly a specialized characteristic. In leaf and bark characteristics *B. nigra* resembles *B. davurica* Pall. of subsection *Albae,* which Tabata (1964, 1966) found to have several characteristics of the *Costatae.* Perhaps these two species occupy an intermediate position between subsections *Costatae* and *Albae.* Obviously, much more work on biosystematics and species cross-compatibility of the Costate birches will be required in order to elucidate their evolution.

NATURAL DISTRIBUTION AND HABITAT

During the Pleistocene the deciduous broad-leaved forests which covered most of eastern North America had to retreat southward ahead of the advancing ice, causing many species to migrate considerably south of their present range. *B. alleghaniensis* had developed into a distinct species by this time, as evidenced by its fossil occurrence at Toronto, Canada, in interglacial deposits of Sangamon age (Berry 1923, Flint 1947). How far south this species penetrated is not known but it may have reached Lee County, Texas. *Betula* pollen in the Lee County bog investigated by Potzger and Tharp (1947) was not identified as to species but it was associated with other mesic genera such as *Acer* and *Tilia,* indicating that it could have been *B. alleghaniensis.* Yellow birch probably persisted throughout the Pleistocene in the unglaciated parts of the Appalachian Mountains (Braun 1950). At the end of the Wisconsin glaciation it moved northward to New York and New England and westward through the Great Lakes region. Yellow birch probably reached the Lake States from the East rather than by migration from the South (Braun 1950).

At present yellow birch ranges from Newfoundland and the Gaspé Peninsula westward through Quebec and Ontario at roughly 48° N latitude to Lake Superior, and to about 95° W longitude in northern Minnesota. From the upper Mississippi Valley it is found southward to southern Wisconsin, northern Indiana, northeastern Ohio, and south in the mountains to eastern Tennessee and northern Georgia. Outliers in southern Minnesota, Iowa, northern Illinois, southern Indiana, and southwestern Kentucky are probably relicts from a different range in the past. Distribution maps published by Gilbert (1960) and Little (1971) show yellow birch as occurring on Anticosti Island and in Manitoba, but according to Dansereau and Pageau (1966) it is not found in either area. These and other adjustments have been made in the map (fig. 1). The northern limit of the species coincides with the isotherm of 2° C (35° F) mean annual temperature. In the West and South the limit is close to the isotherm of 30° C (86° F) annual maximum temperature (Dansereau and Pageau 1966).

Yellow birch grows best on flats and lower slopes, and on moderately well-drained sandy loams of the podzolic and brown podzolic soil groups, but it also occurs on well-drained and on poorly-drained sites. In mountainous terrain, the best growth is on the cooler northern and eastern slopes at elevations up to 760 m (2,500 feet) in New York and New England, and above 910 m (3,000 feet) in the southern Appalachians. In the Lake States, yellow birch grows up to about 490 m (1,600 feet) elevation (Fowells 1965). Yellow birch rarely occurs in pure stands and is more commonly found mixed with hemlock, sugar maple, beech, basswood, red maple, ash or elm. In the eastern part of its range, it is frequently associated with red spruce, paper birch or sweet birch.

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[4] Johnson, A. G. University of Minnesota, St. Paul, Minnesota. Personal communication, January 1962.

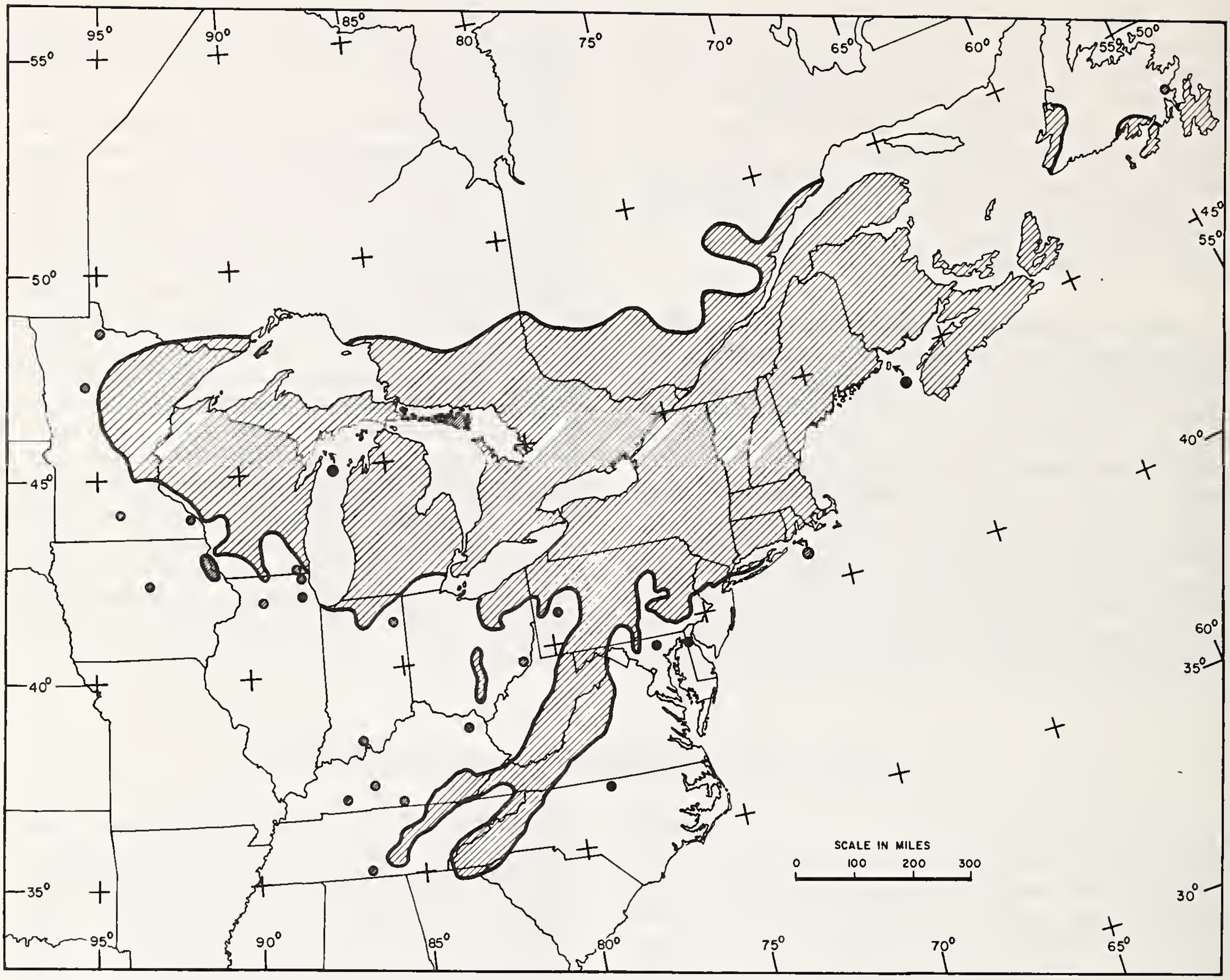

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Figure 1.—The botanical range of *Betula alleghaniensis* Britton.

SEXUAL REPRODUCTION

Reproductive Development

Yellow birch is monoecious with male and female flowers occurring in separate aments or catkins on the same twig. Each catkin contains many small apetalous flowers borne in the axils of bracts or scales. The staminate catkins form during the late summer at the end of long shoots, usually in a cluster of three or more erect catkins. The individual florets of the staminate catkin each contain three flowers, and each flower consists of two or three bilocular anthers (Abbe 1935). Meiosis takes place in August or September, depending on weather and locality, (Woodworth 1929, Dancik and Barnes 1972) and proceeds as far as pollen tetrads in the fall. The following spring these catkins elongate rapidly and become pendent, with the anthers exposed. Pollen shedding proceeds acropetally and usually lasts 3 to 5 days (Dancik and Barnes 1972). In the Lake States it generally occurs during the latter half of May, although it varies from year to year (Ahlgren 1957) and with geographic location.

The solitary pistillate catkins are also formed during the autumn but remain enclosed in the buds during the winter. The buds with female catkins are indistinguishable from vegetative buds and appear terminally on short shoots. Each floret contains three naked flowers and is subtended by a three-lobed bract. Each flower consists of a bicarpellary ovary with two styles (Abbe 1938). The pistillate catkins emerge from the buds in spring with the leaves, usually during the first 2 weeks of May in the Lake States but varying with climatic conditions (Ahlgren 1957) and geographic location (Gilbert 1960). The catkins elongate, the catkin scales separate, and the light-green or reddish styles extend beyond the scales. The pistillate catkins are receptive 2 to 5 days before pollen is released on the same tree (Dancik and Barnes 1972).

Little is known about the fertilization process in yellow birch. In other birches the pollen tubes penetrate the styles within 24 to 48 hours (Hagman 1963), and fertilization apparently takes place 3 to 4 weeks later (Davis 1966). Although the ovary contains two ovules in each chamber, only one ovule usually matures into a seed; the other three abort. The septum between the chambers disappears (Abbe 1935) and the single seed fills the whole fruit, which develops into a samara. For convenience this single-seed fruit will be referred to as a "seed" in this report, as it is in common practice. Occasionally two seedlings will emerge from one seed. Maini and Wang (1967) reported that these "twin" seedlings occcurred at a frequency of 0.12 percent and we have noted them at frequencies from 0.12 to 0.19 percent.[5] The occurrence of these seedlings was attributed by Maini and Wang (1967) to cleavage of zygotic embryos. Because one seedling usually emerges earlier than the other and remains larger, they may not be true twins. More likely these "twin" seedlings result from the occasional fertilization and development of two ovules within one ovary.

Seed dispersal has been reported as early as August 6 in northern Minnesota (Ahlgren 1957) and August 10 in northwestern Pennsylvania (Gilbert 1960), but it usually begins in late September or early October (Burton and Leslie 1952, Gilbert 1960). The seeds continue to fall from the semi-persistent catkins during the late autumn and winter. Benzie (1959) reported that only 12 percent of the seed had fallen by November 13 in northern Michigan while 76 percent fell during October and November in central New Hampshire.[6] Joseph (1929) found that the first seeds to fall had the highest germination capacity, indicating that these may be the well filled and therefore heavier seeds.

The heaviest seeds apparently develop in the central part of the catkin (Redmond and Robinson 1954, Yelenosky[7]). Redmond and Robinson (1954) reported that seed weight depended on catkin size in New Brunswick samples; Yelenosky,[7] who studied a single tree in New Hampshire, also found the heaviest and largest seeds in the largest catkins. Clausen (1968a), however, found no correlation between catkin length and seed size in rangewide collections of yellow birch. Redmond and Robinson (1954) also stated that large seeds had better viability than small seeds, but again we have found no relationship between seed size and germination capacity.[8] Because birch ovaries can develop into apparently normal but empty samaras even in the absence of pollen (Frolova 1956, Clausen 1966), the smaller seeds found in a catkin may be the empty ones.

Yellow birch stands have been observed to begin flowering at the early age of 15 years in Michigan and at 18 to 23 years in northern Wisconsin, but heavy seed crops are generally not produced until the trees are 30 to 40 years old. Trees in the open or along roads may begin to bear seed when they are 11 to 12 years old. One 5-year-old seedling in the Rhinelander nursery had 17 catkins, indicating that certain genotypes have the potential for flowering at an even earlier age. The number of seeds per fruiting catkin, ranging from 121 to 248 and averaging 186, is apparently not closely related to catkin size. The number of catkins appears to decrease from the top to the lower part of the crown, but on the average those in midcrown seem to have the greatest number of seeds per catkin.[9]

Seed production, a characteristic probably under genetic control, varies greatly among individual trees; but because a tree can bear several hundred catkins, yellow birch is usually considered a prolific seeder. Whether provenances differ in seed yield is unknown. Large quantities of seed are produced in well-stocked stands. Gross and Harnden (1968) reported that up to 30 million seeds per acre were produced in Ontario during 1967, an excellent seed year. Some seed is produced in most years, but on the average 1 out of every 10 years is a complete failure and heavy seed crops occur only 1 or 2 years in 10 (Marquis 1969).

Seed quality is usually good in years with a heavy seed crop but poor when the seed crop is light (Marquis 1969). For example, 1963 was a poor seed year in the Lake States and 1964 was a good seed year. Seed of 10 trees in a southern Minnesota stand ranged from 2 to 10 percent and averaged 5 percent germination in 1963, compared with a range of 23 to 77 percent and an average of 45 percent in 1964.[10]. Seed viability depends greatly on weather conditions during pollination, fertilization, and seed development; even in good seed years it varies with local conditions. In 1963, one New Hampshire stand averaged 73 percent germination while another stand less than 40 miles distant averaged only 41 percent. Variation in seed viability among individual trees of the same stand is common. In 1963, seed from 15 trees in a Quebec stand ranged from 1 to 96 percent germination (average 47 percent), while 15 trees in a New Hampshire stand only varied between 60 and 89 percent (average 73 percent).[11] In good seed years germination percentages exceeding 90 percent are common.

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[5] Data on file, Institute of Forest Genetics, North Central Forest Experiment Station, USDA Forest Service, Rhinelander, Wisconsin.

[6] Marquis, David A. 1963. The seeding habits of paper and yellow birch. (Unpublished report on file at the Northeastern Forest Experiment Station, USDA Forest Service, Upper Darby, Penn. 33 p.)

[7] Yelenosky, George. 1959. The strobili and seed of one yellow birch tree. (Unpublished report on file at the Northeastern Forest Experiment Station, Upper Darby, Penn. 36 p.)

[8] See footnote[5]

[9] See footnote[7]

[10] , [11] , See footnote[5]

Compatibility and Crossability

Cross-fertilization is normal in yellow birch stands and self-fertilization is probably rare under natural conditions. Although female catkins tend to be concentrated in the upper part of the crown, male catkins are present there as well; thus, there is no effective spatial separation of the sexes. However, female catkins are usually receptive 2 to 5 days before pollen is shed on the same tree (Dancik and Barnes 1972), a condition tending to prevent self-fertilization.

Self-compatibility varies greatly with the individual genotype. Seed from eight trees tested at Rhinelander, Wisconsin, ranged from 0 to 45 percent germination (Clausen 1966 and [12]). The ability of a particular genotype to set seed after selfing may vary from year to year. Thus, one tree failed to set selfed seed in 1963 but had 45 percent germination in 1964 (Clausen 1966). Germination of outcrossed seed from the same tree ranged from 47 to 51 percent in these 2 years. Indications are that trees with a moderate degree of self-compatibility also produce better seed after outbreeding, but there is as yet no conclusive evidence for this.

Although most intraspecific crosses produce seed, occasional trees have been found to be incompatible (Clausen 1966). Seed viability from these crosses varies considerably. Eight combinations tried at Rhinelander had between 5 and 69 percent germination and reciprocal crosses also differed in viability.[13] Thus, most intraspecific crosses can be expected to set seed successfully, but how good the seed will be cannot be predicted.

Natural interspecific hybridization in the genus *Betula* has been recognized for more than 100 years and appears to be common, demonstrating that reproductive isolation between the species is not complete in this genus. The natural hybrid between *B. alleghaniensis* and *B. pumila* L., a shrubby species, has been known for a long time. Zabel (1895) recognized it among plants he grew from American seeds at Münden, Germany, and it was later described by Schneider (1904) who named it *B.* x *purpusii* Schneider. Further studies of hybrid plants growing in swamps in Minnesota were published by Rosendahl (1916), who concluded that in this area the shrubby parent was *B. pumila* var. *glandulifera* Regel. Recently Dancik and Barnes (1972) have studied the hybrid and its parent species in southern Michigan.

This hybrid is now known from four southeastern counties and one northwestern county of Minnesota and from five counties in southern Wisconsin and one county in northeastern Wisconsin.[14] The hybrid has also been reported from: Lake County, northeastern Illinois (Jones and Fuller 1955); Porter County, northwestern Indiana (Deam 1932); Kalamazoo and Washtenaw counties, southern Michigan (Dancik and Barnes 1972); and Lucas and Stark counties, northern Ohio (Braun 1961). The hybrid has not been reported from the northeastern United States and eastern Canada. However, among material collected for a rangewide study of variation in yellow birch (Clausen 1968a), catkins, bracts, and seeds of one individual in Steuben County, southwestern New York, resembled those of *B.* x *purpusii,* indicating that it may occur in this area as well. Although the two parent species are sympatric in this part of their ranges, they may be phenologically or ecologically isolated, accounting for the relative scarcity of the hybrid in this region. Their period of flowering did, however, overlap in southern Michigan (Dancik and Barnes 1972). The known localities of the hybrid are all close to the southern limits of *B. pumila* and the southwestern limit of *B. alleghaniensis.* Perhaps flowering of the two species overlaps only in this fairly narrow distributional zone where they tend to occupy the same ecological niches.

Another less well-known and apparently fairly rare natural hybrid is the one between yellow birch and paper birch (*B. papyrifera* Marsh.). Gleason (1968) incorrectly assigned this parentage to *B. cordifolia* Regel, which is actually a well defined diploid species (Rosendahl 1928, Brittain and Grant 1965). This hybrid has been found in two northern Minnesota counties,[15] in three northern and three southern Wisconsin localities, and in Hardin County, Iowa.[16] It also occurs in four counties of the Upper Peninsula of Michigan, one county in southern Michigan,[15] and in one county in southwestern New Hampshire.[17] Frequently only one or a few hybrid trees are found in each location, but in Marathon County, Wisconsin, seven individual hybrids have been recognized in the same stand.[16]

Crossing of the two species apparently takes place more often than the reported frequency of mature hybrids would indicate. When seedlings from 55 yellow birch seed sources included in a rangewide variation study (Clausen 1968b) were raised in the nursery at Rhinelander, Wisconsin, putative yellow x paper birch hybrids appeared in 32 seed sources ranging from Georgia to Quebec and from Newfoundland to Minnesota. The frequency of hybrids was less than 1 percent in 25 sources, 1 to 2.5 percent in four sources, and 6.5, 8.3, and 17.2 percent in one source each.[18] The three sources with high proportions of hybrids came from northwestern Minnesota, northern Illinois, and central Iowa, respectively—all at the extreme western limit of yellow birch. These outliers all contained more paper birch than yellow birch; thus the greater availability of paper birch pollen may have favored hybridization. Although yellow birch tends to flower later than paper birch (Ahlgren 1957), there is apparently sufficient overlap in the flowering of the two species to permit hybridization to take place over practically all of the yellow birch range. One probable reason that so few mature hybrids have been reported is that the hybrid seedlings have difficulty getting established and competing with other tree seedlings. Another possible reason is that the trees have not been recognized as hybrids.

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[12],[13],[14], See footnote[5], p. 5.

[15], Barnes, B. V. University of Michigan, Ann Arbor, Michigan, Personal communication, April 1971.

[16], See footnote[5], p. 5.

[17], See footnote[2], p. 1.

[18], See footnote[5], p. 5.

Because sweet birch (*B. lenta*) and yellow birch appear to be related and are sympatric over most of the sweet birch range, natural hybrids between these species could be expected. Eames (Harger *et al.* 1917) felt that specimens from western Connecticut were hybrids and Braun (1961) suggested that such hybrids may occur in northeastern Ohio. Sharik (1970), however, found no sweet x yellow birch hybrids in his survey of the two species in the Appalachian Mountains, although their flowering periods showed some overlap. Thus, if this hybrid does occur, it is much rarer than the other two natural hybrids mentioned.

In summary, yellow birch exhibits a moderate degree of self-compatibility and varying amounts of intraspecific incompatibility. It shows some interspecific crossability under natural conditions, and it can be crossed artificially with several other species, which is discussed later in this publication.

Controlled Pollination Techniques

Difficulties in climbing large trees and other technical problems limit the usefulness of field pollination. Yellow birch twigs are very slender, and therefore light, fragile isolation bags must be used. The bags are difficult to attach securely and movement of the branches by the wind often punctures the bags.

A much more convenient method is to collect 40 to 60 cm. long branches (usually in mid-February at Rhinelander, Wisconsin) and to graft them onto seedling rootstocks in the greenhouse using the bottle graft technique. Within 10 days to 2 weeks the female catkins appear and can be bagged. Pollination can be done a few days later. Advantages of this method are: (1) The avoidance of contamination because the work is done before any birch pollen is released in nature; (2) the convenience of working at ground level; (3) the independence of weather conditions; and (4) the ease of removing bags for checking of female flower receptivity and pollen application.

Bagging should be done as soon as the female catkins emerge from the buds. Glassine or parchment paper bags are suitable isolation bags. In the greenhouse the bags are tied on with paper- or plastic-coated wire so they can be readily removed and replaced. In the field they can be held on with plastic-coated wire or by stapling them tightly around the cotton-wrapped branch portion. Male catkins are easily removed or can be enclosed in the bag with the female catkins if selfing is desired. Up to 10 catkins can be accommodated in a single bag.

Yellow birch pollen is easily forced on cut branches placed in water in a greenhouse. The time required for forcing depends on how long before natural shedding the branches are cut (Johnson 1945). If the branches are collected in early February and kept at 20° C. and a 20-hour photoperiod, the pollen will shed in 2 to 3 weeks. Thus, branches collected about 2 weeks prior to grafting will shed pollen in time for pollination.

Pollen in cotton-stoppered vials can be stored with little loss of viability in a dessicator over Drierite[19] ($CaSO_4$) at 3 to 4° C. for at least 1 year. Viability can be tested using the agar or hanging-drop technique with 10 to 20 percent sucrose in the medium (Johnson 1943). Yellow birch pollen will also germinate in distilled water and can be counted after 24 to 48 hours at 20° to 30° C.

Pollination in the greenhouse is done by removing the bag and applying the pollen with a short camel's-hair brush kept in the vial throughout the pollination period. Because all the female catkins within a bag do not develop at the same rate, it is convenient to be able to take the bag off and check on their receptivity. Each catkin should be pollinated again 2 days after the first pollination to ensure that all the flowers in a catkin receive pollen near their peak of receptivity, otherwise the yield of filled seeds will be reduced. The isolation bags, which are replaced after each pollination, can remain on the branches for 10 to 14 days after the last pollination.

Field pollination can be done with a small disposable syringe or similar pollen applicator. Repollination is particularly critical in the field, where it is difficult to judge receptivity of the female flowers. In order to prevent loss of seed from early-maturing catkins, it is advisable to cover them at the time of debagging with bags made of nylon mesh or fiberglass screening.

Seed Germination and Nursery and Field Establishment

Yellow birch seeds have been stored successfully for 4 years at an average moisture content of 5 percent at 2° to 4° C. (Clausen 1965). Storage up to 8 years is possible but individual seed lots vary greatly in how well they maintain their viability (Clausen 1970a).

Seed dormancy can be overcome by stratification or by light treatment. Long photoperiods are known to promote germination of birch seeds (Vaartaja 1959) and unstratified yellow birch seeds will germinate in water under light (Yelenosky 1961), apparently because a water-soluble inhibitor is leached out of the pericarp and broken down by exposure to light (Black and Wareing 1959). Both fresh and stored seeds are easily tested for germination by placing them on moist perlite in petri dishes held at 20° C. with a 20-hour photoperiod for 30 days (Clausen 1965). Although yellow birch seed will germinate at 10° C. (Tubbs 1965), Vaarama[20] reported much better germination at 20° C. Red light (650 mu) promotes germination but treatment with blue-green light (490 $m\mu$) for 24 to 48 hours is almost as effective[20]. Germination begins about 10 days after sowing and is essentially complete after 24 days. Valuable seed is routinely germinated at Rhinelander, Wisconsin, in glass-covered dishes; the germinants are transplanted into soil while still in the cotyledon stage.

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[19] The use of trade names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Agriculture of any product to the exclusion of others which may be suitable.

Seedlings respond well to long-day treatment (Vaartaja 1957). Warm-white or cool-white fluorescent tubes supplemented with incandescent bulbs are superior to Gro-lux[21] tubes for yellow birch growth (Marquis 1965). At a daylength of 20 hours under greenhouse conditions, yellow birch seedlings will reach a height of 40 to 50 cm. in 3 months, but even better growth can probably be obtained in a CO_2 enriched atmosphere (Krizek *et al.* 1969). Raising seedlings in the greenhouse in containers such as polyethylene bullets (Stanek 1970), "Jiffy-7"[21] peat pellets or Japanese paper pots[22] also looks promising.

An alternative method of handling a large number of experimental seed lots is to sow the seed in flats in late winter, cover it with moist peat and hold the flats at 2° to 4° C. for 4 weeks before moving them to a shadehouse (Clausen 1968b). Germination begins after about 10 days and is almost complete within 2 weeks. If the seedlings are then given supplementary light to provide an 18-hour photoperiod, they can be transplanted into a nursery 3 months after the end of stratification.

Fall sowing of the seed, either broadcast or in drills, in fumigated seedbeds is the recommended nursery practice. Nursery fertility criteria, optimum bed density, and minimum stock sizes for the species are given by Hanks (1969). Seedlings reach their best development under half-shade (Logan 1965). Growth can be accelerated by the use of plastic greenhouses (Phipps 1969).

Experimental plantations for genetic studies or seed orchards should be established on good planting sites. Yellow birch appears to be extremely sensitive to competition from grass and other herbaceous vegetation, and it cannot be planted successfully in grassy fields. If planting in the open is desired the site should be clean-cultivated before planting and kept weed-free for at least 2 years after planting. Best results have been obtained by using large nursery stock (average height 50 cm.), hand planting in the spring, and fertilizing annually for several years after establishment. Yellow birch seedlings planted in the open are subject to heat injury on the basal part of the stem. This problem can be avoided by placing a 10 cm. (4-inch) high collar of aluminum foil around the stem base.

Underplanting in pole-sized stands of northern hardwoods is also being tested in the Lake States. The original stands were thinned to 25 to 30 sq. ft. of basal area, all slash removed, and advance regeneration and brush sprayed with herbicides. Stock, planting methods and fertilization were the same as described for planting in the open. Competing herbaceous vegetation has been controlled manually and chemically. Competition from sprouts and other woody vegetation is becoming a problem but can be controlled. The residual overstory will be removed gradually as the need arises. Experience from these plantings and other planting trials indicates that it may be desirable to retain more overstory than suggested above, perhaps up to 50 sq. ft. of basal area. The denser overstory would probably reduce herbaceous competition, reduce the danger of frost, and provide the desired 50-percent shade. Small-scale trials also suggest that top pruning may aid in the establishment of yellow birch planting stock (Godman and Mattson 1971).

All experimental field plantings of yellow birch should be fenced against deer and rabbits, a costly but necessary procedure (Richards and Farnsworth 1971). Development of effective and inexpensive means of protecting individual trees would be a desirable alternative. Rodent control may also be necessary.

ASEXUAL REPRODUCTION

In nature, yellow birch reproduces almost exclusively by seeds. The species is essentially nonsprouting (Solomon and Blum 1967) although seedlings and young trees will sprout from stumps (Fowells 1965).

Budding is widely used for vegetative propagation of fruit trees and ornamentals but rarely for forest trees. This technique, although used successfully by Pauley (1948) for budding *B. alleghaniensis* on seedlings of *B. populifolia* Marsh., does not appear practical except for experimental purposes such as transmission of virus diseases, etc.

Rooting of dormant birch cuttings is very difficult. Greenwood cuttings will root more readily, but the degree of success depends greatly on the time the cuttings are taken, rooting media, growth regulators, and individual biotypes. Gabriel (1961) reported that 34 percent of yellow birch greenwood cuttings taken on July 21 and 22 rooted when treated with Hormodine No. 3 (a commercial root-promoting preparation containing 0.8 percent indolebutyric acid) and placed in perlite under mist. Percentage of rooting success varied with individual trees from 7 to 63. Cuttings from 24- and 45-year-old trees rooted better than those from either younger or older trees, but none of the rooted cuttings survived the winter. Birch cuttings acquire tree shape from the start regardless of where in the crown they are taken (Fröhlich 1961).

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[20] Vaarama, Antero. Induced mutations and polyploidy in birch, *Betula* spp. Final Report (Part V), PL-480 Project E8-FS-47 Grant No. FG-Fi-133, 100 p. 1970.

[21], See footnote[19], p. 7.

[22] Schneider, Gary. Michigan State University, East Lansing, Michigan, Personal communication, May 1971.

Air layering of yellow birch has apparently not been attempted but may be a feasible method of vegetative propagation. This technique has been used successfully on other birch species with 1 or 2 percent concentrations of indolebutyric or indoleacetic acid (Fröhlich 1957, Clausen and Kraus 1961). As with cuttings, the critical step is to establish the propagules after they are severed from the parent trees (Fröhlich 1957).

Yellow birch can be propagated readily by grafting. Various methods have been used, including cleft, whip, side-veneer, and bottle grafts (Klaehn 1961). The last two are the preferred methods.

The side-veneer graft is simple to make and gives excellent results when mass propagation of particular biotypes is desired. The rootstock should be well established. For greenhouse grafting, 1- or 2-year-old seedlings should be potted in late spring of the year prior to grafting. When the rootstock is brought into the greenhouse in mid-January, root activity begins in about 3 weeks. The stock plants are ready for grafting about 1 week later when the buds begin breaking.

The scions should have two to three buds and should preferably be cut from the last season's growth, but older wood can be used if necessary. A long, vigorous shoot can safely be divided into several scions if the terminal end of each scion is covered with wax or a similar grafting compound. The scions are held in place with raffia or rubber strips. The union should be covered with Treekote[23] or a similar paste-type grafting compound. The ties are usually removed in 6 to 8 weeks. Growth of the scions is improved if the grafts are maintained on an 20-hour photoperiod. The top of the stock plants should be cut back gradually; they can be completely removed about 3 months after grafting or before the grafts are moved outside the greenhouse.

Bottle grafts used in controlled pollination work can be made in the greenhouse in mid-February. The rootstock must be larger than that used for side-veneer grafts in order to accommodate the fairly large brances used as scions. The 40 to 60 cm. long scions are tied to the stock plants with an elastic plastic tape completely covering the union. No waxing or other covering is necessary. Waxed paper cups or other disposable containers can be substituted for the standard glass bottles. About one-half cm. should be cut off the basal end of the scions once a week to avoid xylem plugging and the water should be changed weekly. Due to the width and elasticity of the grafting tape there is little danger of injury to the grafts, and release is, therefore, less critical than for side-veneer grafts. The top of the stock plants should also be removed more slowly than from side-veneer grafts.

Grafting success is usually excellent except when scions come from very old trees. In these cases, if a few ramets can be established it is easy to make secondary grafts with vigorous scions taken from these ramets. Yellow birch has been grafted successfully on yellow birch, paper birch, and river birch rootstock. Although no scion-rootstock incompatibility has appeared so far, it is probably safest to use yellow birch stock. There are no reports of intraspecific grafting incompatibility in this species. Birch grafts acquire tree shape without difficulty (Fröhlich 1961).

Field grafting of yellow birch has apparently not been attempted, but grafting in the spring just as the buds begin to show green may be possible as this is often used for grafting of ornamental birches (Krüssmann 1943). Scions can be stored satisfactorily for a limited time in plastic bags in a refrigerator or packed in snow outdoors. Whether long-term storage is possible, for example, in a freezer, is unknown.

GENETICS AND BREEDING

Phenotypic Variation in Natural Stands

Leaf Morphology

Dancik and Barnes (1972) took detailed measurements of spur-shoot leaves of 70 yellow birches in a southern Michigan stand and reported considerable variation among the trees in all characteristics studied. They also found much variation in leaf size within an individual tree, whereas leaf shape, number of marginal teeth, and number of lateral veins were relatively constant.

Dancik (1971) studied leaf variation in trees from 118 populations in Michigan, Wisconsin and Minnesota. Spur-shoot leaves from the lower inside crown were found to be the most uniform. All 19 characteristics studied showed much variation among trees. There were significant among-population differences for each characteristic but the populations could not be arranged into consistent groups on the basis of single-character analyses. Canonical variates analysis demonstrated a relationship between leaf morphology and site characteristics of the populations. Multivariate analyses, however, did not show any direct relationship between geographic proximity of the populations and their relative morphological similarity.

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[23] See footnote[19], p. 7.

Catkin, Fruit and Pollen Characteristics

Biosystematic studies of yellow birch morphology have emphasized catkin and fruit characteristics. A rangewide variation study of 52 stands demonstrated significant differences among stands in catkin length, five bract characteristics and three fruit characteristics. Catkin length, measured on the central axis or rachis, was not correlated with any of the other characteristics. As expected, the bract characteristics were intercorrelated as were the fruit characteristics. Fruit length, however, was only weakly correlated with bract length (Clausen 1968a).

Within-stand variation was greater than variation among stands in all characteristics except the relative length of the bract and fruit length/width ratio, demonstrating that much individual tree variation exists in this species. Dancik and Barnes (1972), who studied 66 trees in one southern Michigan stand, also reported much variation among trees in bract shape and noted that these bracts were less pubescent than those of northern Michigan trees. Within-tree variation was small for all nine characteristics studied by Clausen (1968a). All characteristics were either independent of, or at best weakly correlated with environmental factors of the stand locations. Thus, catkin and fruit characteristics in yellow birch appear to vary in a random manner and do not show any obvious trends in geographic variation, indicating that there may be little selection pressure on these characteristics (Clausen 1968a).

Dancik and Barnes (1972) found some variation in pollen diameter of 70 southern Michigan trees, and they also reported that many trees had polyporate pollen instead of the triporate condition common in most birches.

Bark Characteristics

Yellow birch bark varies in color from light yellow on very young trees through yellowish-brown to reddish-brown or almost black on old trees. In New England a silvery gray color is so typical, on young trees at least, that the species is commonly referred to as "silver birch."[24] The bark is at first smooth but soon separates into thin, papery curls. Exfoliation tends to increase with age and size of the trees, although some trees retain an essentially smooth bark as they grow larger. Clausen and Godman (1969) reported that rough-barked trees tend to be older and slower growing than trees with smooth or peeling bark. Rough-barked trees on the average took twice as long to reach 4 inches in diameter at breast height and were more than twice or even three times as old as trees of equal diameters with smooth or peeling bark (fig. 2). Bark thickness was more closely related to age than to tree diameter or bark type (Clausen and Godman 1969). Dancik and Barnes (1971) studied bark variability of 25 trees in a 60-year-old stand in northern Michigan and found no relationship between degree of exfoliation and tree diameter. However, no rough-barked trees were included in their study. Although bark characteristics may be influenced by site, the phenotypic variation observed can more likely be attributed to genotypic variation among the trees. It seems clear that trees having rough, furrowed, or plated bark are very old or slow-growing, and therefore undesirable as crop trees or superior tree candidates.

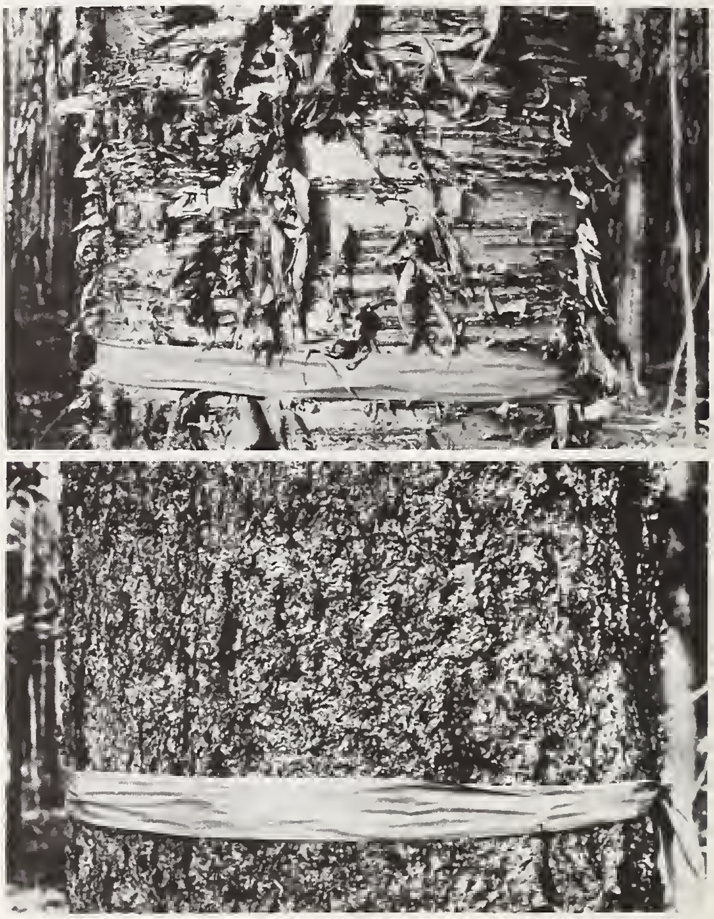

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Figure 2.—Two yellow birches growing within 150 feet of each other. The tree with peeling bark (upper) is 15.2 inches d.b.h. (ribbon) and 72 years old; the tree with rough bark (lower) is 14.8 inches d.b.h. (ribbon) and 162 years old.

Tree Growth and Quality Characteristics

Falkenhagen[25] investigated 233 individual trees in 27 yellow birch populations in the province of Quebec and reported continuous variation in all characteristics studied. He found that trees of the same age increased in height from northeastern to southwestern Quebec. Using a classification system with seven crown types, he reported that crown shape became poorer with increasing latitude and to a lesser degree with increasing altitude. Number of epicormic branches also increased from south to north. A small study of five Laurentian populations indicated that stem straightness may be associated with crown shape, epicormic sprouting and branch angle. However, variation in straightness and roundness of the trunk and branch angle was fairly small. In general, both growth and form tended to be best in southwestern Quebec.

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[24] Johnson, A.G., University of Minnesota, St. Paul, Minnesota. Personal communication, September 1971.

[25] Falkenhagen, E. R. Génécologie du boleau jaune (*Betula alleghaniensis* Britt.) - Localisation et description sylvicole preliminaire des arbres-parents. Can. Dept. Fish. & For., Quebec Reg., For. Res. Lab. Unpubl. Rep. Q-16, 32 p. - tables, fig., and appen. June 1969.

Initiation and Cessation of Growth

Length of the growing season varies over the range of yellow birch from 70 to 185 days and growth of the species varies accordingly. Sharik (1970) found that yellow birch populations at about 670 m. (2,200 feet) elevation in southwestern North Carolina flushed 3 to 4 weeks earlier than populations growing at the same elevation in northern New Hampshire. The low-elevation North Carolina populations also flushed 3 to 4 week earlier than populations at 1585 m. (5,200 feet) elevation at the same latitude. It has been demonstrated that once chilling requirements have been met, temperature is the most important environmental factor controlling growth initiation of yellow birch (Pauley 1954, Wang and Perry 1958). Sharik (1970), however, postulated that in environments with large diurnal temperature fluctuations, such as high mountains, selection for flushing at longer daylength has occurred. If so, photoperiod would interact with temperature to prevent flushing until the danger of freezing night temperatures has passed.

Sharik (1970) also reported that growth cessation took place earliest in high-elevation populations in Vermont and New Hampshire and latest in low-elevation populations in southwestern North Carolina and southwestern Virginia. The inverse relationship between time of growth cessation and latitude indicates that photoperiod is the major factor controlling growth cessation and onset of dormancy in this species. However, the inverse relationship between growth cessation and elevation suggests that some other factor, possibly temperature, is also involved.

Genetic Variation Among Provenances

Few provenance studies of yellow birth are underway at this time. Early results indicate that much variation is present in the species.

Nursery Studies

One study at Rhinelander, Wisconsin, included 55 provenances representing the entire geographic range of the species. A summary of the variation in 24 seedling characteristics observed in the nursery is presented in table 1. The provenances differed significantly in all characteristics except root length of 1-year-old seedlings.

Survival

Only minor differences in survival were noted after the second year in the nursery. Although differences among the provenances increased during the third year, survival was essentially independent of their origin (table 1). Due to the large number of entries, even small correlation coefficients in table 1 are statistically significant. The low values, however, indicate that there is no close relationship between the variables in question. Some of the material was also grown in nurseries at Houghton, Michigan, and at Syracuse, New York. Survival was poorer at these locations than at Rhinelander, and there was little agreement in the ranking of the individual provenances at the three nursery locations. However, survival at Houghton and at Syracuse showed no closer relationship to provenance than at Rhinelander.

Winter Injury

All provenances showed some degree of winter injury after their second winter in the Rhinelander nursery. Damage was generally light in most northern and eastern provenances. Most severely damaged were seedlings from low elevations in Tennessee, Ohio, and southern Indiana, as well as those from Kentucky and Virginia (Clausen and Garrett 1969). As expected, percentage of trees with winter injury was inversely correlated with latitude of the provenances, and it showed some association with average January temperature and length of growing season (table 1). Sharik (1970), on the basis of growth cessation data, calculated an index of potential freeze damage for Appalachian yellow birch populations grown in southern Michigan. However, with a reported difference between extremes of only 3 percent, the index appears to be of little value. Certainly the results of the rangewide study demonstrate that this index does not give a reliable estimate of the winter hardiness of the individual provenances.

Growth

Although the provenances differed significantly in height and dry-matter production of 1-year-old plants, these characteristics were not closely related to environmental variables at their origins (table 1). As pointed out previously, several of the correlations in table 1 are statistically significant but biologically meaningless. Seedlings from West Virginia and Lower Michigan grew almost twice as much as those from the poorest provenance during their second year

TABLE 1—Summarized analyses of variance of 24 characteristics measured on 55 nursery-grown provenances of yellow birch and correlations with environmental variables of the provenances[1]

Characteristic and age	F value	Correlation (r) with environmental variable						
		Lat.	Long.	Elev.	Grow. season	Annual precip.	Ave. July Temp.	Ave Jan. Temp.
1 Year:								
Plant height	[2] 10.68**	−0.525**	0.353**	0.350*	0.459**	[3] —	0.416**	0.498**
Root length	n.s.	—	—	—	—	—	—	—
Root dry weight	2.88**	—	—	—	—	—	—	—
Leaf dry weight	4.41**	−.319	—	—	.270*	—	.356**	.308*
Stem dry weight	4.35**	—	.316*	—	—	—	—	—
Top dry weight	4.48**	—	.297*	—	—	—	.285*	—
Plant dry weight	4.07**	—	—	—	—	—	—	—
Top/root	2.33**	.434**	—	—	.405**	—	.343*	.307*
2 Years:								
Survival	1.64*							
Height growth	2.53**	—	—	—	—	—	—	—
Plant height	4.35**	−.350**	—	.298*	—	—	—	.362**
No. of branches	4.66**	−.351**	.435**	—	.348*	—	.519**	—
Branch length	3.04**	—	—	—	—	—	.274*	.276*
Branch angle	2.35**	—	.307*	—	—	—	—	—
Leaf length	1.60*	—	—	—	—	—	—	—
Leaf width	1.91**	.479**	—	—	−.436**	—	−.401**	−.420**
Leaf length/width	10.00**	−.718**	—	.411**	.488**	.559**	.454**	.702**
Leaf dry weight	1.93**	.429**	—	—	−.516**	—	−.503**	−.356**
Growth cessation	2.21**	−.782**	—	.484**	.561**	.517**	.627**	.676**
3 Years:								
Survival	2.20**	.300*			−.327*			—
Winter injury	4.86**	−.675**			.540**			.623**
Leaf flushing	7.87**	.846**	—	−.618**	−.654**	−.517**	−.575**	−.757**
Plant height	2.20**	—	—	—	—	—	—	—
Stem diameter	1.85**	.405**	—	—	.414**	—	−.315*	−.350*

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[1] Data on file, Institute of Forest Genetics, NCFES, Rhinelander, Wisconsin.

[2] * and ** = Significant at the 5 percent and 1 percent level, respectively.

[3] — = Nonsignificant; blank space = not tested.

in the nursery, but annual height growth was independent of environmental variables (Clausen 1968b). Total plant height after the second growing season showed a similar lack of pattern. At the end of the third growing season, seedlings from the Lower Michigan provenance were twice as tall as those from the two low-elevation Tennessee provenances, but the variation in height among provenances appeared to be random (Clausen and Garrett 1969).

Seedlings of a number of provenances were also distributed to nurseries at Houghton in Upper Michigan, East Lansing in Lower Michigan, and Syracuse, New York. The performance of seedlings from 25 provenances grown at all four locations are compared in table 2. There were significant differences in 3-year-height among provenances at all locations. Much provenance x nursery interaction is also apparent, but no clear trends are evident (table 2). The fact that the Lake States nurseries are located near the northwestern extreme of the species range and the Syracuse nursery is situated at about midrange may explain some of the differences in provenance performance. Apparently climatic conditions in the three Lake States nurseries differ enough to account for the dissimilar performance of the provenances at these locations. As at Rhinelander, plant height at Houghton, East Lansing, and Syracuse was not correlated with environmental variables of the provenances. Thus, it appears that variation in seedling height is essentially random.

A study of 46 Quebec provenances substantiated that seedling height at 2 years of age is essentially unrelated to longitude and latitude of their origin, again indicating a random pattern of variation. Large differences were also noted among populations originating from relatively small areas, demonstrating

TABLE 2—Plant height of 25 yellow birch provenances after 3 years in the nursery as a percent of the nursery mean

Provenance number	State or Province	Location		Nursery			
		Lat.	Long.	Houghton[1]	Rhinelander[1]	East Lansing[2]	Syracuse[1]
3241	Nova Scotia	46.6	60.5	85	122	102	114
3065	Nova Scotia	45.4	61.8	89	85	96	94
3066	New Brunswick	47.4	65.2	112	102	111	100
3001	Quebec	49.2	65.4	82	91	90	54
2997	Quebec	47.0	70.3	88	86	93	58
2999	Quebec	47.4	72.6	104	102	108	114
3000	Quebec	47.5	75.0	99	91	114	94
2977	Maine	44.8	68.6	126	87	90	148
2956	Maine	43.7	70.9	98	100	114	112
2985	New Hampshire	44.0	71.4	100	96	123	81
2982	Vermont	44.7	72.6	105	119	93	95
2971	Massachusetts	42.7	73.2	132	104	93	102
3312	Pennsylvania	41.6	78.7	108	125	108	83
3299	Virginia	37.8	79.1	107	84	117	195
2959	North Carolina	35.7	82.3	96	114	108	71
2954	Tennessee	35.7	85.3	78	64	72	88
2958	Indiana	38.3	86.5	88	96	72	124
2983	Illinois	41.9	89.4	102	92	129	86
2960	Michigan	45.9	84.8	94	107	108	85
2987	Michigan	47.0	88.7	110	99	87	72
3298	Wisconsin	45.7	89.0	107	92	102	124
2963	Wisconsin	43.1	88.4	122	107	90	103
2964	Minnesota	44.2	94.1	83	108	90	82
2966	Minnesota	47.6	92.5	94	119	102	129
2967	Minnesota	47.8	90.2	92	108	93	91
Average height (cm.)				37.3	45.9	101.8	29.5

[1] Based on all trees in the sample row.

[2] Based on the tallest tree in each row.

that much local variation apparently exists in this species.[26] Sharik[27] tested 23 Appalachian Mountain provenances in southeastern Michigan and also found little correlation between 3-year height and latitude or elevation of the provenances.

In the 55 provenances studied at Rhinelander there was generally a good correlation between seedling height and diameter (r = + 0.85**). Although seedlings of northern origin tended to be thicker than those of southern origin, diameter was only weakly correlated with latitude and length of growing season (table 1), indicating that seedling diameter may also vary randomly (Clausen and Garrett 1969).

Branch and Leaf Characteristics

Significant provenance differences in number of branches, branch length, and branch angle were recorded at Rhinelander, but the variation in these characteristics was small and appeared to be random (table 1). Branch characteristics were measured on 2-year-old seedlings, and it is possible that variation in branch habit is not readily apparent at this age and may become more pronounced with time. Whereas only minor differences in leaf size of 2-year-old seedlings were noted, leaf shape appeared to show clinal variation with southern provenances having narrower leaves than northern ones (table 1). Dancik (1971) also found Appalachian Mountain trees to have narrower leaves than those from the western Great Lakes region.

Chilling Requirements

Experimental evidence indicates that there is geographical variation in chilling requirements for breaking of terminal shoot dormancy. Wang and Perry (1958) tested provenances from the entire range of the species and reported that winter chilling at 3° to 4° C. (38° to 40° F.) was required for early and normal breaking of dormancy. Trees from northern provenances, however, needed about twice as long a period of chilling as did those from southern provenances. Under normal weather conditions at Gainesville, Florida, most unchilled plants eventually leafed out near the base of the stem while the terminal remained dormant for periods ranging from a few months to 1 year. Variation in chilling requirements is apparently clinal, with northern trees requiring more chilling for normal bud-break and stem elongation than southern trees.

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[26] Corriveau, Armand Can. For. Serv., For. Res. Lab. Ste-Foy, Quebec. Personal communication, June 1971.

[27] , See footnote[2], p. 1.

Growth Initiation

Wang and Perry (1958) found that growth initiation in winterchilled plants was correlated with the latitude of origin. Trees from northern provenances began growth earlier in the spring than did those from farther south. Photoperiod had no effect on budbreak, except in certain unchilled plants that flushed earlier when exposed to long days. In the 55 provenances tested in the nursery at Rhinelander, flushing also showed a high correlation with latitude and good correlations with average January temperature and length of growing season (table 1), indicating that variation in time of growth initiation is clinal (Clausen and Garrett 1969). Trees from Quebec and New Brunswick began growth first. Those from coastal New Brunswick and Newfoundland provenances flushed somewhat later, followed by trees from provenances further south and west along the Appalachian Mountains. However, there are some exceptions to this gradual pattern of development, probably related to adaptation to local climatic conditions.

Flushing of trees from 10 provenances grown in the Rhinelander nursery for a study of within-provenance variation was followed for 2 years. The greatest difference among the provenances was observed on April 28 in 1970 and on May 7 in 1971. The small variation in time of flushing is probably due to different weather conditions in the 2 years. As expected, time of growth initiation was closely related to latitude of seed origin (r = + 0.93** in 1970 and + 0.96** in 1971), and there was a high degree of repeatability between years (r = + 0.92**). Average April temperature at the point of origin also strongly affected flushing, as indicated by correlation coefficients of -0.84** for 1970 and -0.85** for 1971.[28]

Although the clinal variation pattern in flushing is significantly related to latitude and to climatic factors closely associated with it, such as average January temperature, average April temperature and length of growing season, other environmental factors are also involved. Elevation of the seed origin apparently has some effect (table 1). Trees from high-elevation Virginia and Kentucky provenances flushed later than those from more southern provenances (Clausen and Garrett 1969). In the 23 populations from the Appalachian Mountains raised by Sharik (1970) at Howell in southern Michigan, high-elevation North Carolina and Virginia samples also leafed out later than lower-elevation samples from similar latitudes. Elevation, on the other hand, did not show any effect in New Hampshire and Vermont populations. This may mean that although temperature is the major environmental factor affecting growth initiation, in high-altitude montane habitats with large diurnal temperature fluctuations there has been a selection for genotypes responding to long photoperiods, resulting in later budbreak. Photoperiod thus appears to interact with temperature to prevent damage from low night temperatures in these habitats. Such a photoperiodic response has been demonstrated in high-elevation Douglas-fir populations by Irgens-Möller (1957); Sharik (1970) suggests that a similar mechanism may be operative in yellow birch as well.

Growth Cessation

Time of shoot growth cessation was reported by Wang and Perry (1958) to be inversely correlated with latitude, indicating that photoperiod is the major factor controlling growth cessation and onset of dormancy. Similar results were obtained from the rangewide provenance test at Rhinelander, which demonstrated that geographic variation in time of growth cessation is clinal (Clausen 1968b). Trees from the northeastern part of the range are the first to stop growing, followed progressively by those from further southwest in the Appalachian Mountains. Similarly, trees of northern Lake States origin generally stop growing earlier than those from farther south. However, populations from west-central Wisconsin and northern Lower Michigan continue to grow much later than populations from similar latitudes in the east.

Sharik (1970) studied 21 populations from the Appalachian Mountains and found that growth cessation of seedlings from the extremes of latitude overlapped. However, he reported more overlap of populations from different elevations at the same latitude than of populations from latitudinal extremes. Thus, trees from a 1585 m. (5,200-feet) elevation North Carolina source ceased growth 9 days earlier than those from a 670 m. (2,200 feet) source, but there was a 50-percent overlap between individuals of the two populations. When populations from about 910 m (3,000 feet) elevation were compared, there was no overlap between a North Carolina and a New Hampshire population. Sharik (1970), therefore, found that the correlation between time of growth cessation and latitude improved when latitude was corrected for elevation. Although growth cessation showed some association with elevation in the rangewide test at Rhinelander (table 1), the relationship was not consistent; correcting the latitude for elevation did not result in a better correlation between latitude and growth cessation.

All provenances tested at Rhinelander, except one from Virginia, had completed 50 percent of their total height growth by July 13, 1966. Two weeks later, five northern provenances had already completed 90 percent of their seasonal growth.[29] The differences among provenances in rate of growth appear to be poorly related to total plant height and to growth cessation.

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[28] , See Footnote[5], p. 5.

The length of the period between growth cessation of the earliest and the latest provenances differs from year to year, but the variation pattern remains essentially the same. Growth cessation of trees from the 55 provenances took place over a period of 17 days during their second year in the Rhinelander nursery (Clausen 1968b), but extended over 26 days during the third year, when only 11 provenances were studied. The correlation coefficient for growth cessation of the 11 provenances in the 2 years was + 0.82**, indicating a high level of year-to-year repeatability. Similarly, time of growth cessation of 10 provenances studied in 1970 was correlated with provenance latitude ($r = -0.78^{**}$); however, a Georgia provenance only continued to grow an average of 12 days longer than a Quebec provenance.[30] Sharik (1970) reported a difference in growth cessation of 31 days between the earliest and the latest of the 21 provenances he tested. Because his tests were conducted in a different year than the Rhinelander tests and more than 3 degrees of latitude farther south, it is not surprising that growth cessation extended over a longer period in his material.

Concentration of Wintergreen Oil

The wintergreen oil in the inner bark of yellow birch contains 99 percent methyl salicylate which occurs in the form of a glucoside that requires enzymatic action to release the ester (Guenther 1949). Preliminary results indicate geographic variation among provenances in the concentration of wintergreen oil.[31] Steam distillates from the bark of trees from 15 provenances were analyzed by gas chromotography. Southern populations appeared to have greater concentrations of oil per volume of bark than northern ones, and eastern populations may contain more oil than western ones. However, much within-provenance variation was also observed. Size of the individual seedlings sampled had no effect on the amount of oil present, but there were indications of seasonal differences. Much more work is needed, however, to establish the variation pattern in wintergreen oil concentration in yellow birch.

Field Tests

Yellow birch provenance tests have only been in the field for 4 years; thus only preliminary results from the rangewide test of 55 provenances are presented below.

Survival

Two low-elevation Tennessee provenances and provenances from Kentucky and Ohio have shown uniformly poor survival after 3 years in the field. These were always among the five provenances with the poorest survival record at test locations in Michigan, Wisconsin, New York, Ontario, and New Brunswick. Otherwise the provenances varied greatly in survival, and much interaction between provenances and test areas was apparent.

The provenance from southern Indiana has not been hardy either. Two southern provenances had good survival at Syracuse, New York, but had only average to poor survival at all other locations. In contrast, some northern provenances survived poorly at Syracuse. Some mild-climate provenances survived better in the maritime climate of New Brunswick than at other test areas. On the other hand, provenances from the mild climate of eastern Canada did not necessarily have poor survival in the harsher climate of the Lake States. A few northern provenances had better than average survival in all test areas and were among the six best in at least one location.

Growth

Although growth in the field in Northern Wisconsin has not yet been measured, trees from West Virginia and New York provenances so far appear to grow as well or better than those of Wisconsin, Minnesota, and Quebec origin. In the Upper Peninsula of Michigan, the North Carolina and Iowa provenances seem to perform better than Lake States provenances. However, these are general observations only; the performance of the provenances cannot be evaluated until the trees have been measured and their further growth and development assessed. An example of rapid, early growth of one provenance is shown in figure 3.

Radiation Sensitivity

Provenances appear to differ in sensitivity to gamma radiation. Trees from 10 widely separated provenances were planted in a gamma field at Rhinelander, Wisconsin, in the spring of 1968. Yellow birch is much more resistant to both chronic and acute radiation than coniferous trees (Sparrow *et al.* 1965, Sparrow and Sparrow 1965), but 93 percent of the birches died when exposed for three growing seasons to a dose-rate of 100 roentgen (R) per 20-hour day. All of the control plants, which received 0.3 R/20-hr. day, survived. Survival at dose rates ranging from 2.5 to 50 R/20-hr. day was variable. LD_{50} exposures[32] for the provenances varied from 24 to 58 R/20-hr. day. These values were much lower than the LD_{50} of 83 R/day after 3 years of exposure reported for yellow birch by Sparrow *et al.* (1970). This discrepancy may be due to the use of different material at a different location, and possibly differences in experimental

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[29],[30],[31]. See footnote[5], p. 5.

[32] LD_{50} = Lethal dosage 50 percent. The dosage at which survival is reduced to 50 percent of that of the control.

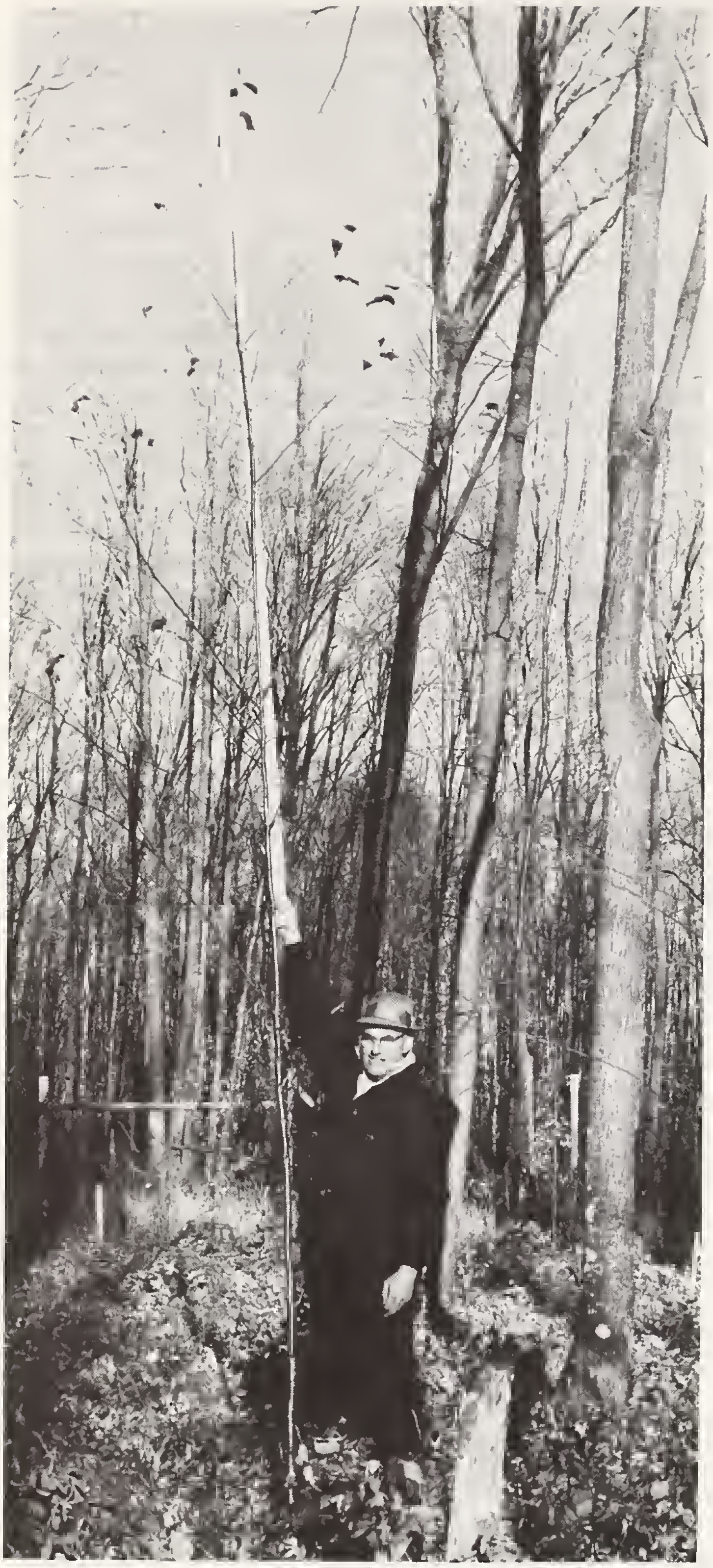

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Figure 3.—This seedling of a northern Lower Michigan provenance had a total height of 525 cm at the end of its fifth growing season in the field. Chequamegon National Forest, northwestern Wisconsin, October 17, 1972.

and cultural techniques. Survival after exposure to gamma radiation varies with provenance but no patterns are evident.

Height of the plants was reduced in direct relation to the amount of radiation received. After 3 years of exposure during the growing season, plants receiving 100 R/20-hr. day were on the average only 29 percent as tall as the control plants, while those receiving 2.5 R/20-hr. day were 93 percent as tall as the controls. Trees from the northern Wisconsin provenance that showed the best survival also had the least reduction in height growth, and thus appeared to be most resistant to radiation. However, with the exception of the Wisconsin provenance there was no consistent relationship between survival and growth reduction. The response to gamma radiation thus appears to vary randomly among the provenances.

Genetic Variation Within Provenances

Growth

Progenies originating from wind-pollination have been used in studies of genetic variation within provenances. A study at Rhinelander includes 199 progenies representing 21 widely separated provenances. Height differences between the best and the poorest progenies at 1 year of age ranged from 23 percent in a southern Nova Scotia provenance to 127 percent in a New Brunswick provenance (Clausen and Garrett 1969). When all progenies were compared there was a difference of 402 percent between the tallest and the shortest progenies. At age 2, progenies from an eastern Quebec provenance had the least difference in height (32 percent); a western Quebec provenance showed the greatest variation, with 158 percent. The difference between the tallest and the shortest of all progenies amounted to 230 percent. At the end of the third year in the nursery the southern Nova Scotia provenance showed only a 19 percent difference between the tallest and the shortest progenies. A northern Nova Scotia provenance, with a 93-percent progeny difference, had the most within-provenance variation. The greatest overall difference among progeny means was 152 percent. Much year-to-year variation in ranking of individual progenies from the same provenance was also noted.

When variance components were calculated for 138 open-pollinated families, 34.6 percent of the variation in 2-year height was due to differences among provenances and 22.6 percent was due to differences among families. The provenance component was reduced to only 3.0 percent for 3-year height while the family component increased to 34.6 percent, indicating that the within-provenance variation may be increasing with time while the variation among provenances seems to be decreasing. A similar trend was observed in the range-wide provenance test; i.e., variation in height among the provenances decreased from ages 1 through 3.

Narrow-sense heritability of tree height, based on 40 trees from each of 138 open-pollinated progenies at ages 2 and 3, was estimated to be 0.679 and 0.689, respectively.[33] If height growth of the trees in future years should be highly correlated with their juvenile height, early selection for height would be profitable. However, the reliability of these early results is unknown. Much of the among-provenance variation observed in the rangewide provenance study can probably be ascribed to within-provenance variation. However, the great amount of provenance x nursery and provenance x test-site interaction may indicate that the performance of the provenances can change with location and time. Thus, juvenile and mature characteristics could turn out to be poorly correlated.

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[33], See footnote[5], p. 5.

A study of 379 Quebec progenies from 46 stands also demonstrated that much within-provenance variation exists in yellow birch. When five progenies from each stand were compared, differences in 2-year height between the best and the poorest progenies were as low as 21 percent in one stand from La Verendrye Park and as high as 75 percent in another one from a nearby location in the park. Within-provenance differences (based on 10 progenies per stand) ranged from 36 percent in a stand from the St. Lawrence valley near Quebec to 96 percent in one from the vicinity of Lac St. Jean. The most variable provenance had a difference of 288 percent between the tallest and the shortest progenies. The greatest over-all difference between progeny means amounted to 293 percent.[34]

Growth Initiation

Time of bud-break was followed in five progenies from each of 10 provenances in the Rhinelander nursery for 2 years. The provenances differed in mean flushing time, but there was considerable overlap among the progenies. Individual seedlings showed even greater overlap; some seedlings of the latest-flushing provenance were as far advanced as some late seedlings of the earliest-flushing provenance in both years. Sharik (1970) reported a similar situation in Michigan. He found that 9 percent of the seedlings of an early-flushing New Hampshire population overlapped with a late-flushing North Carolina population.

In the Rhinelander study, the amount of within-provenance variation differed considerably not only among the 10 provenances but also from year to year within the same provenance. The difference in average flushing score (on a 5-point scale) between the earliest and latest progenies in 1970 was only 0.26 points for a Quebec provenance but 1.20 points for a Nova Scotia provenance. In 1971 the situation was reversed. The Quebec progenies differed by 1.06 points while the Nova Scotia progenies were less variable with a difference of 0.46 points. These two provenances had the least and the most within-provenance variation in 1970, but in 1971 a Wisconsin provenance was the least variable and a New Brunswick provenance the most variable. However, because the scores are based on sight estimates of the amount of flushing, some of the variation and the apparent year-to-year reversal may be the result of the scoring system.

Growth Cessation

Growth cessation was recorded in six progenies from each of 10 provenances during their third year in the nursery. The provenances differed significantly from each other in average date of growth cessation but their progenies overlapped considerably (fig. 4). There was no overlap between progeny means of the two geographically most widely separated provenances. The latest Quebec progeny stopped growing before the earliest Georgia progeny, but individual seedlings of the two provenances showed some overlap. Sharik (1970), in his test of 21 Appalachian provenances in Michigan, also found that seedlings from the extremes of latitude included overlapped with respect to time of growth cessation.

The provenances tested at Rhinelander differed considerably in the amount of within-provenance variation. The earliest progeny of a Virginia provenance stopped growing 13 days before the latest progeny—a difference as great as that between the average dates of growth cessation for the northernmost and the southernmost provenances. In contrast, the difference between the earliest and the latest progenies was less than 5 days in a New Hampshire provenance (fig. 4). However, progeny differences were only significant at the 5-percent level in provenances from Maine and southern Minnesota. These results and those of Sharik (1970) suggest that within-provenance variation is less for time of growth cessation than it is for time of growth initiation. However, growth initiation in both tests was estimated on a five-point scale, while growth cessation was measured at regular time intervals; thus a comparison of variation in the two phenological events may be invalid.

Variation in Seedling Morphology

In 0.04 percent of germinating yellow birch seedlings examined by Maini and Wang (1967), the cotyledons emerged from the pericarp before the radicle. We have observed this type of abnormal germination with an average frequency of from 0.3 to 0.8 percent in seeds collected for a rangewide provenance test.[35] Seedlings with an abnormal number of cotyledons have appeared in germination tests at frequencies up to 0.08 percent for one cotyledon, 0.08 percent for three cotyledons, and 0.005 percent for four cotyledons. Fused cotyledons have occurred at frequencies of 0.08 percent and very narrow cotyledons at 0.017 percent. Abnormal cotyledon shapes observed at very low frequencies in rangewide seedling populations included: Fused, short and broad, narrow, narrow and split, split, and heart-shaped.

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[34], See footnote[26], p. 13.

[35], See footnote[7], p. 5.

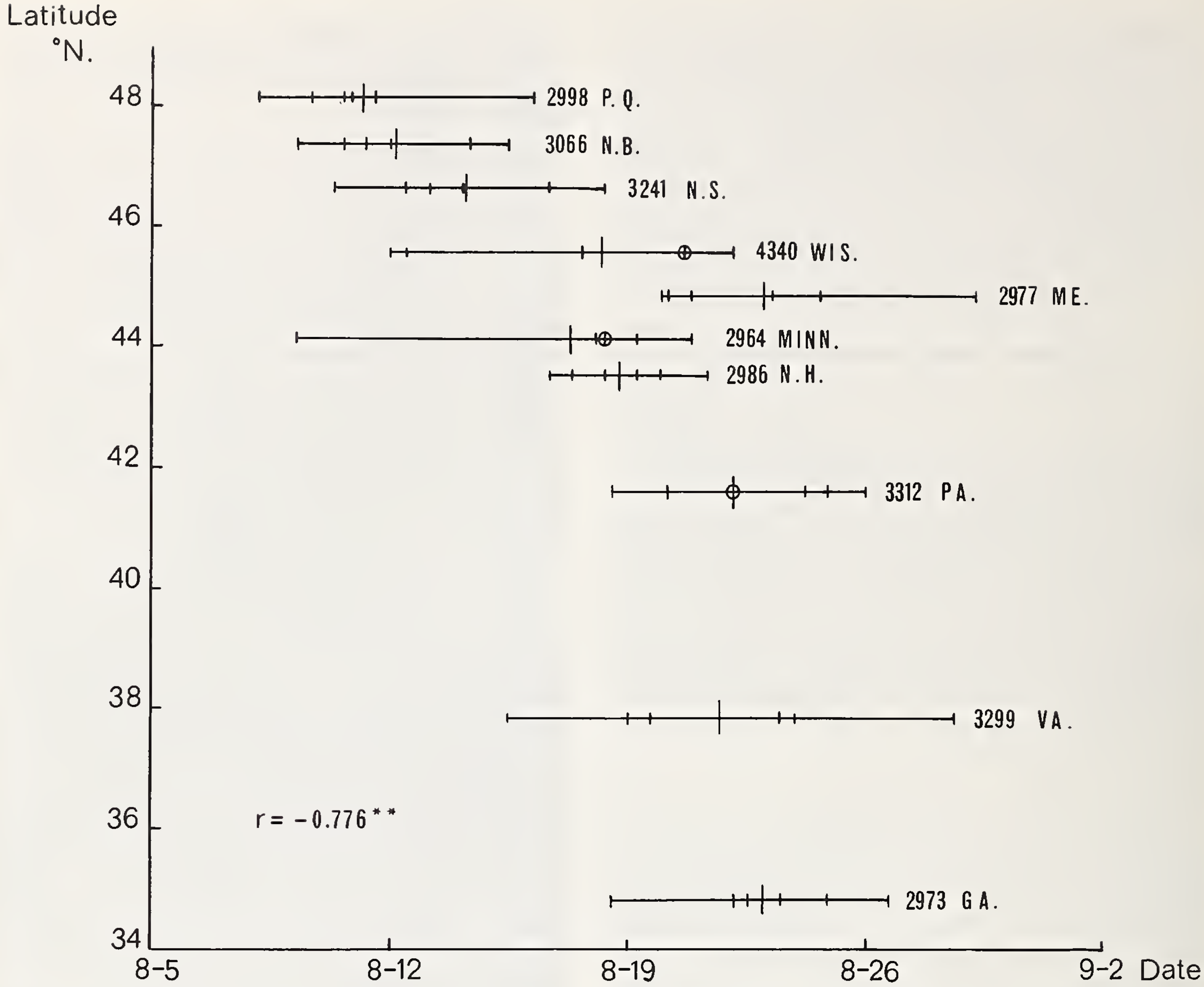

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Figure 4.—Within-provenance variation in growth cessation. Short and long lines mark progeny and provenance means, respectively. Circles indicate places where two mean values coincide.

A few albinos have also been noted and seedlings with yellow-green and greenish-white cotyledons have appeared at average frequencies of 0.036 and 0.017 percent, respectively. Additional chlorophyll deficiencies observed in the rangewide material included: Cotyledons with white tips, white bases, or a white band across central part, one white and one partially white cotyledon, one green and one partially white cotyledon, cotyledons with yellow tips, yellow centers, or yellow-green tips. Whether these cotyledon abnormalities represent mutations or have resulted from other causes is unknown, but similar aberrant types have appeared after seed irradiation. Vaarama[36] reported an increase in chlorophyll deficiences and smaller cotyledons after yellow birch seed had been exposed to 10,000 R of gamma radiation. Leaf abnormalities also increased with increasing dose-rates.

Occasional seedlings with many short branches have been noted (fig. 5). Plants with similar branching habit have appeared from seed irradiated with 15,000 R of gamma rays.[36]

Interspecific Hybridization

The fact that yellow birch is known to hybridize with a few other species in nature does not necessarily mean it can be readily crossed with most other species in artificial hybridization attempts. Nor are the progeny produced necessarily true interspecific hybrids.

Early interspecific crosses with yellow birch as female or male parent were carried out in the Arnold Arboretum by Woodworth (1931). He reported that several crosses set seeds containing embryos but whether seedlings were grown from these seeds is un-

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[36] Vaarama, Antero. Induced mutations and polyploidy in birch, *Betula* spp. Final Report (Part II), PL-480 Project E8-FS-47 Grant No. FG-Fi-133, 81 p. 1968.

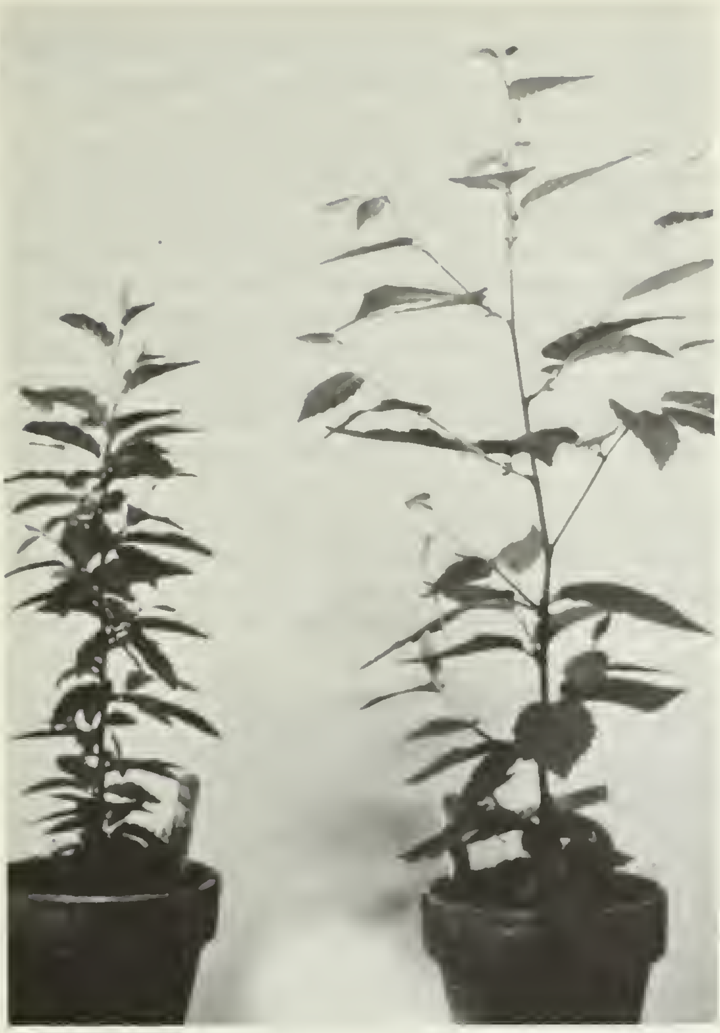

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Figure 5.—Variation in branch characteristics between two open-pollinated siblings. Seedling on left has numerous short branches; the one on the right has normal branching habit.

known. Five of the combinations attempted by Woodworth have subsequently been repeated by other workers and hybridity has been verified for four of them. Two combinations have not yet been repeated, and therefore remain unverified. Smith and Nichols (1941), who also worked in the Arnold Arboretum, apparently produced seedlings from several attempted crosses. One of these combinations, *B. alleghaniensis* x *B. lenta*, had previously been tried by Woodworth (1931) and was later attempted by Schreiner (1949) and Clausen (1970b). The progenies produced have all resembled the female parent and are probably not true hybrids. More likely they result from contamination or apomixis.

The results of attempted crosses between *B. alleghaniensis* as female parent and male parents of varying ploidy are summarized in four groups below:

Attempted crosses	*Authority*
1. Crosses easy to make, hybridity verified:	
B. alleghaniensis (6x)	
x *B. papyrifera* (4-6x)	Woodworth (1931), Clausen (1970b)
2. Crosses possible, hybridity verified:	
B. alleghaniensis (6x)	
x *B. pumila* (4x)	Woodworth (1931), Clausen (1970b)
x *B. glandulosa* Michx. (2x)	Clausen (1970b)
3. Crosses difficult to make, hybridity not verified:	
B. alleghaniensis (6x)	
x *B. lenta* (2x)	Woodworth (1931), Smith and Nichols (1941), Schreiner (1949), Clausen (1970b)
x *B. nigra* (2x)	Clausen (1970b)
x *B. ermani* (4x)	Clausen (1970b)
x *B. grossa* (6x)	Woodworth (1931), Johnson[17]
x *B. populifolia* (2x)	Clausen (1970b)
x *B. pubescens* Ehrh. (4x)	Clausen (1970b)
4. Unsuccessful crosses:	
B. alleghaniensis (6x)	
x *B. pendula* Roth (2x)	Tucovic and Jovanovic (1969), Clausen (1970b)

For comparison, the results of attempted crosses with *B. alleghaniensis (B. all.)* as the male parent are summarized in the following four groups:

Attempted crosses	*Authority*
1. Crosses easy to make, hybridity verified:	
B. lenta (2x)	
x *B. all.* (6x)	Schreiner (1949), Clausen (1970b), Sharik and Barnes (1971)
B. pendula (2x)	
x *B. all.* (6x)	Vaclav (1961), Vaclav (1969), Clausen (1970b)
2. Crosses possible, hybridity verified:	
B. davurica (4x)	
x *B. all.* (6x)	Woodworth (1931), Johnson[17]
B. papyrifera (4-6x)	
x *B. all.* (6x)	Woodworth (1931), Clausen (1970b)

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[17] See footnote[4], p. 3.

B. nigra (2x)	
x *B. all.* (6x)	Clausen (1970b)
B. populifolia (2x)	
x *B. all.* (6x)	Clausen (1970b)
B. pubescens (4x)	
x *B. all.* (6x)	Johnsson (1945), Tucovic and Jovanovic (1969), Clausen (1970b)
3. Crosses difficult to make; hybridity not verified:	
B. maximowicziana Regel (2x)	
x *B. all.* (6x)	Woodworth (1931)
4. Unsuccessful crosses:	
B. ermani (4x)	
x *B. all.* (6x)	Clausen (1970b)
B. pumila (4x)	
x *B. all.* (6x)	Clausen (1970b)
B. glandulosa (2x)	
x *B. all.* (6x)	Clausen (1970b)

Many putative artificial hybrids tend to resemble their female parent, indicating that they are probably not true hybrids. Johnsson (1945) reported that seedlings produced in Sweden from the cross *B. pubescens* x *B. alleghaniensis* were matroclinous and similar results have been obtained in this country.[38] Tucovic and Javanovic (1969) also found six progenies of the same cross to be *pubescens*-like. However, in progenies of four other mother trees, 57 to 88 percent of the seedlings resembled *B. alleghaniensis*. Nearly all the interspecific crosses listed above for which hybridity has not been verified have so far resembled the female parents morphologically, suggesting that they may be products of apomixis. Apparently the presence of foreign pollen is sufficient to stimulate embryo development even though there may have been no fusion of gametes.

Taxonomic subdivisions presumably indicate that species of the same subsection are more closely related to each other than to members of other subsections. Hence, greater crossability might be expected within than between subsections. However, crosses between yellow birch and other *Costatae* were generally less successful than crosses involving members of the *Albae*. Thus far, better crossability has been observed between than within subsections in *Betula* (Clausen 1970b). Differences in chromosome numbers of the parental species appear to be of greater importance than taxonomic subdivisions in determining crossability. In general, when the hexaploid yellow birch is crossed with either diploid or tetraploid species, the crosses having yellow birch as male parent are more successful than the reciprocal crosses. Crosses between low ploidy females and high ploidy males are commonly more successful than reciprocal crosses in this genus (Clausen 1970b).

Although some crosses may show hybrid vigor when young, this superiority is not always maintained with age. Five-year-old *B. lenta* x *B. alleghaniensis* hybrids produced by Schreiner (1949) were reported to be 42 percent taller than yellow birch and 10 percent taller than sweet birch of the same age. When measured at 27 years of age the hybrid trees averaged 8 percent shorter and 22 percent smaller in diameter than intraspecific crosses of the parent species (Sharik and Barnes 1971). The intraspecific yellow birch and sweet birch crosses did not differ significantly from each other in height and diameter. Vaclav (1969) reported that *B. pendula* x *B.alleghaniensis* hybrids were about as tall at age 9 as intraspecific crosses of the female parent. Young

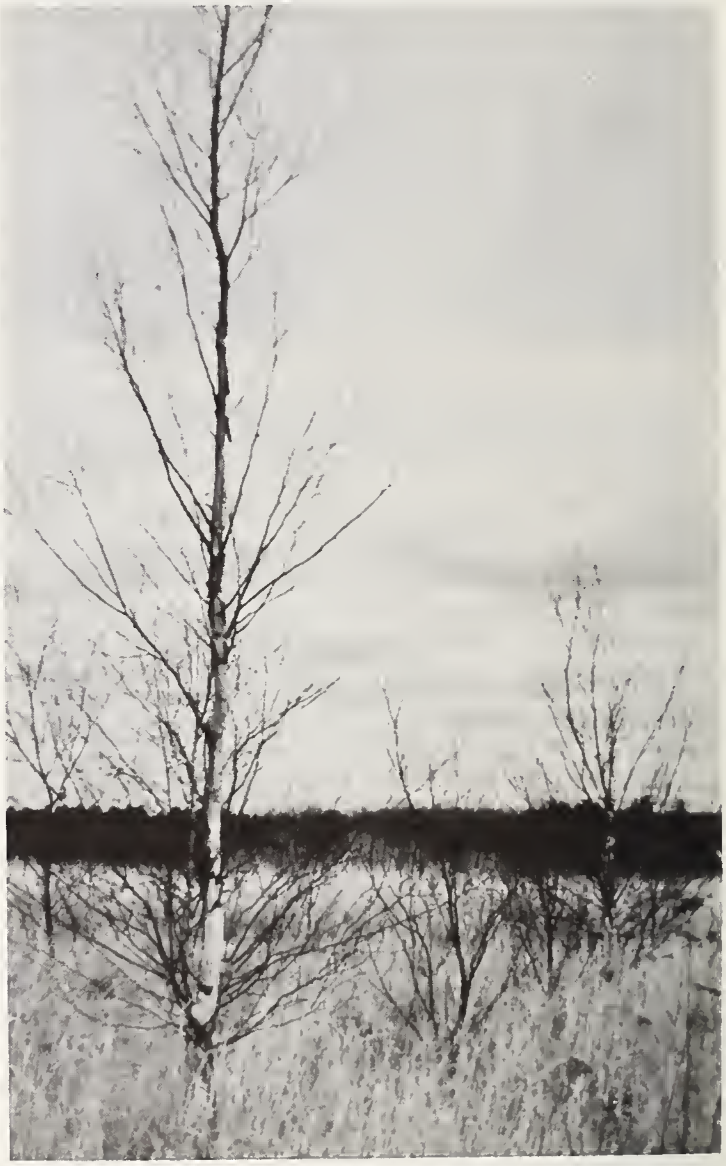

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Figure 6.—Segregation in F $_1$ progeny of *Betula davurica* x *B. alleghaniensis*. First and fourth trees in the row resemble female parent; second and third trees resemble male parent.

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[38], See footnote[5], p. 5.

plants of the same parentage have performed similarly at Rhinelander. Tucovic and Jovanovic (1969) found that 2-year-old *B. pubescens* x *B. alleghaniensis* hybrids on the average were no taller than control seedlings of *B. pubescens*. Seedlings of the cross *B. alleghaniensis* x *B. papyrifera* have usually been taller than the female parent but shorter than the male parent. The reciprocal cross has also been superior to *B. alleghaniensis* but has only equaled *B. papyrifera* in height. The *B. davurica* x *B. alleghaniensis* hybrids have segregated into vigorous *davurica*-types and less vigorous *alleghaniensis*-types (fig. 6). Thus, none of the interspecific hybrids produced so far with yellow birch as one parent have shown any definite hybrid vigor.

Cytogenetics

Yellow birch, as pointed out previously, is a hexaploid species, usually with 84 chromosomes (2n). Woodworth (1929), however, reported some counts as high as 98. Preliminary work on provenance material has given counts of 84 for most provenances but a range from 54 to 98 chromosomes was noted.[39] Thus, there may be intraspecific variation in the chromosome number of the species. Whether the variation is geographic, local, or of individual tree origin must await the results of further studies. Vaarama[40] reported counts of 84 in normal plants of Wisconsin origin and about 160 in a plant germinated in colchicine. Dancik and Barnes (1972) were only able to get chromosome counts of two of the trees they studied in southeastern Michigan. Both trees had 84 chromosomes. Woodworth (1929) reported somewhat irregular meiosis with lagging chromosomes and cytomixis in the material he examined in the Arnold Arboretum. Later, however, he found meiosis to be normal in material from Minnesota (Woodworth 1930). Dancik and Barnes (1972) also reported normal meiosis and cell division in two Michigan trees.

IMPROVEMENT PROGRAMS

The objectives of a tree improvement program should be tailored to the desired end-use of the species. Yellow birch produces high-quality wood with attractive grain and desirable physical properties. Because yellow birch wood is much in demand for veneer, paneling, furniture, flooring, cabinets and millwork, veneer logs and high-grade sawlogs are high-value products. At present, the annual cut of these logs exceeds annual growth and the demand is expected to increase (Quigley and Babcock 1969). Coupled with the increasing demand is a rapid decrease in the supply of high-quality logs. Although yellow birch has good growth potential, other faster growing hardwood species are economically better suited for pulp, chipboards, and similar products. For the above reasons, a yellow birch breeding program should focus on improving the quality as well as the growth rate of the trees.

Tree improvement is essentially exploitation of the existing genetic variation. Tree breeders can accomplish this goal through several methods of genetic improvement. These include: (1) Selection of superior trees, (2) selection of superior provenances, (3) hybridization of superior individuals selected within provenance tests or progeny evaluations, (4) provenance hybridization and (5) species hybridization.

Criteria for phenotypic selection of superior yellow birch trees were developed by Clausen and Godman (1967). Because improved tree quality is the principal breeding objective, the first selection should be for quality characteristics. For the stem, these include straightness, roundness, taper, grain, self-pruning, and absence of defects, and for the crown, apical dominance, branch angle, and branch diameter. Secondary consideration should be given to growth characteristics such as tree height, stem diameter, and growth rate as well as volume, length, diameter, and density of the crown (fig. 7). Because yellow birch typically occurs in uneven-aged stands of mixed species composition and no plantations are available, comparison of the selected trees with neighboring trees is probably of little value. A diameter growth rate of at least 0.2 inch per year is recommended in the selection guide (Clausen and Godman 1967); however, this is probably conservative since some trees apparently are capable of growing about 0.5 inch per year (Schreiner 1970). Trees with smooth or extensively peeling bark appear to be faster-growing than rough-barked trees of the same age (Clausen and Godman 1969).

All superior tree candidates should be evaluated before they are used in an improvement program. This is particularly important in a species such as yellow birch in which, as shown previously, individual tree variation is large. The evaluation can be accomplished in several ways; progeny testing and advanced-generation selection are two common methods. In the first, the superior trees serve as parents in half-sib and full-sib matings and are evaluated on the basis of the performance of their progenies. The best parents are then incorporated into a seed orchard. However, with a species as variable and as sexually precocious

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[39] See footnote[6], p. 5

[40] Vaarama, Antero. Induced mutations and polyploidy in birch, *Betula* spp. Final Report (Part III). PL-480 Project E8-FS-47, Grant No. FG-Fi-133, 95 p. 1969.

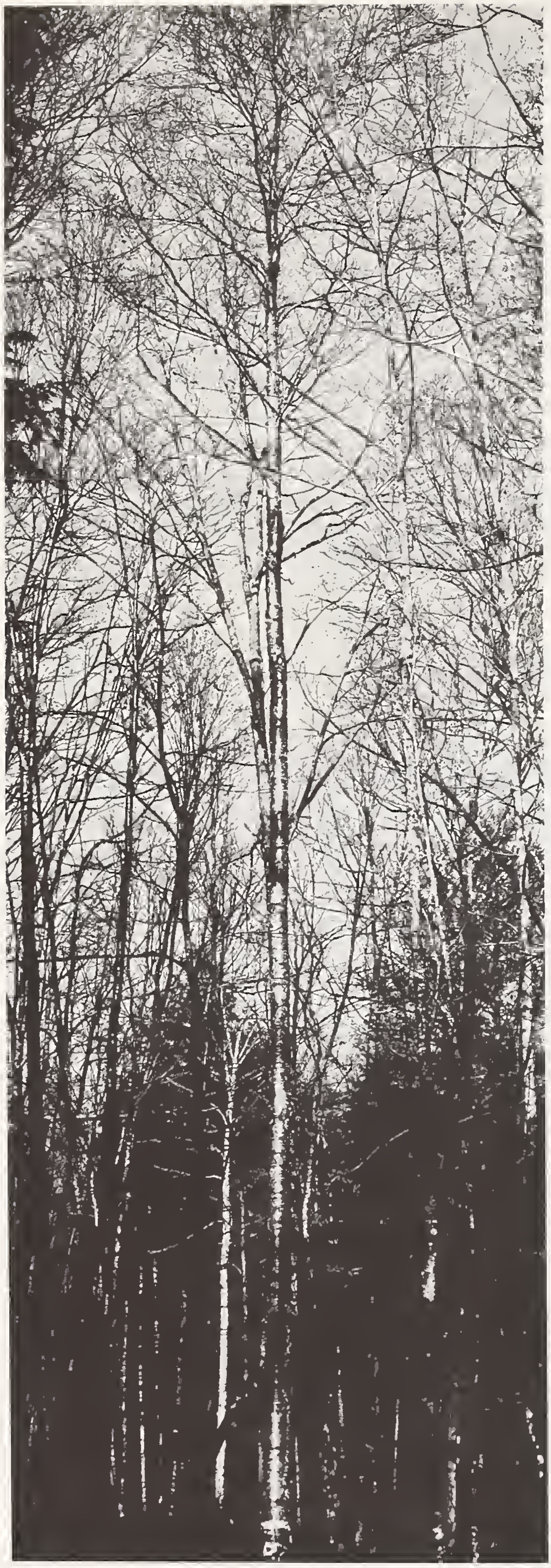

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Figure 7.—This superior yellow birch has a well-pruned, round stem with little taper. The crown is well-proportioned, shows excellent apical dominance, has small branches, good branch angles, and high density.

as yellow birch, advanced-generation selection is preferred because of the faster progress that can be made with this method. An improvement program undertaken by the USDA Forest Service in New England uses this approach and will serve as an example of a recommended procedure.

The objective of the program, which employs family selection with subsequent roguing, is to produce genetically improved seed for the Green Mountain National Forest in Vermont and the White Mountain National Forest in New Hampshire. Twenty superior phenotypes have been selected on the Green Mountain National Forest and 25 on the White Mountain National Forest. These will be tested together with the following numbers of superior trees from other areas: five from Pennsylvania, 10 from West Virginia, 25 from the Lake States, and 10 from Ontario and Quebec. The purpose of including trees from other areas is to broaden the genetic base and to identify possible superior genotypes of nonlocal origin. Seedlings will be grown in replicated plots in a New Hampshire nursery for 3 years. Field tests will be established in two locations on each of the two New England Forests, and in one location each on the Allegheny National Forest in Pennsylvania and the Monongahela National Forest in West Virgina. Randomized complete blocks with four-tree plots and eight replications will be used. Each test planting will be surrounded by a deer-proof fence. Early measurements of the progenies will include total height, number of branches, and presence of forks. Later evaluations will be on the basis of tree height and diameter, height to first fork, merchantable height and stem quality.[41]

Two test plantings, one each on the Green Mountain and the White Mountain National Forests, will be established with the goal of their future conversion into seed orchards. On the basis of third-year height in the nursery, the best 50 percent of the families will be chosen for inclusion in the seed orchards. This selection should be made with caution. It is conceivable that at this age many nonlocal families would perform better than the majority of the local families, which would therefore be excluded. However, because we as yet have no information about correlations between juvenile and mature performance, it would be unwise to choose only the tallest families without regard for origin. To ensure that local families which may outgrow nonlocal families later in life are represented, about one-half of the families to be included in the seed orchards should be of local origin. Within the selected families only the tallest 10 percent of seedlings without forks will be used.

The seed orchards will be rogued according to the performance of the families in the evaluation plantations. Roguing is scheduled for 15 years after planting, when all the poorest families will be removed. If thinning becomes necessary before that time, the poorest trees within each family will be cut. All the plantations can be converted into seedling seed orchards after evaluation, if desired, using the roguing criteria outlined above. Dawson and Pitcher (1970) recommended the same improvement method; *i.e.*, selection of superior phenotypes, family selection, and conversion of the test plantings into seed orchards, for yellow birch in the North Central States. Trees in seedling seed orchards will probably begin to flower 10 to 15 years after planting.

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[41] Dorn, Donald E. Plan for the progeny testing of selected yellow birch (*Betula alleghaniensis* Britton) on the Green Mountain National Forest, White Mountain National Forest (On file at Regional Office, USDA Forest Service, Milwaukee Wisconsin.)

How effective nursery selection will be in yellow birch is uncertain at this time. Neither progenies nor individual seedlings included in the open-pollinated tests at Rhinelander showed much year-to-year consistency in height ranking during 3 years in the nursery. However, because nursery selection for seedling size has proven effective in other birches (Clausen 1963), it may well be that the selected seedlings will maintain their superior height growth and good form in future years. The high heritability estimates obtained for seedling height in the test at Rhinelander indicates that selection for height growth should be successful. The use of the largest seedlings will be advantageous for practical reasons because of their greater ability to withstand competition from other vegetation.

All the superior trees being tested in the Forest Service program will also be vegetatively propagated and the ramets established in a breeding arboretum for use in a full-sib progeny test. The choice of clones to be used in this test will depend on the performance of the families in the open-pollinated progeny evaluation. When the trees have been evaluated on the basis of both tests, the breeding collection can be rogued and used as a clonal seed orchard.

Recommendations for the maintenance of seed orchards are not yet available. However, the ground should be kept free of weeds for the first few years by clean cultivation, mulching or application of herbicides. Later a good ground cover should be established and kept mowed. Fertilization will doubtless be advantageous, but what types, how much will be needed, and whether it will stimulate or increase seed production are unanswered questions. We do not know how the trees will develop under these conditions, and whether pruning or shaping for greater ease of seed collection will be necessary.

Because the provenance tests currently in progress are very young, it is impossible to predict whether any provenances will turn out to be superior to local provenances. Although trees from local provenances were well above average in height after 3 years in nurseries at Syracuse, New York, and Houghton, Michigan, those from some other provenances were considerably taller. In the Rhinelander nursery, the local provenance was only 88 percent as tall as the nursery average and was exceeded by 43 other provenances. Local provenances have usually had better than average survival in the field tests, but only rarely have they been the best survivors. Their early height growth has not been exceptional either. However, until superior nonlocal provenances have been recognized in long-term tests, it is probably safest to plant stock from a good local provenance or perhaps mix stock from a slightly more southerly origin with that from a local source. Because there is much within-provenance variation in yellow birch, it is unlikely that use of a particular provenance will result in as much improvement as the use of seed from progeny-tested superior trees.

Evidence accumulated so far indicates that within-provenance variation is much greater than variation among provenances. For this reason, hybridization between widely separated provenances will probably be most productive if selected individual trees are used as parents. The recommended procedure would be to select superior individuals within available provenances, propagate the selections by grafting, and plant the ramets in a seed orchard. The selections should be evaluated on the basis of full-sib progeny tests and the orchard should then be rogued to remove the poorest selections. A similar approach can be used if progeny evaluation plantings are available. For example, the best individuals within the best 10 percent of the families could be selected and vegetatively propagated for use in a seed orchard. The seed produced by the clones would represent a considerable genetic improvement over average commercial seed. If desired, seed harvested from the clones could be used for a second cycle of family selection and propagation, resulting in a breeding population producing seed of proven genetic quality.

On the basis of existing evidence, genetic improvement through species hybridization does not appear promising. While the gain from this approach theoretically is great, much more research is needed to evaluate its potential.

How should genetically improved seed be used? Artificial regeneration of yellow birch by seeding or planting has not been adequately tested and most early attempts have failed, primarily due to poor choice of sites, unsuitable techniques, and lack of protection against animals (Bjorkbom 1969). Until successful techniques for establishing and maintaining yellow birch plantations have been developed, improved seed should not be used for direct seeding or planting on unimproved sites. Instead, it is recommended that the seed be used to produce large plants (3 to 4 feet tall) in the nursery, which can then be planted at a rate of 100 to 150 per acre in small openings on the best northern hardwood sites. The plants should be individually protected against animals and be given maximum care. This approach would be safe and efficient and should result in the production of a large number of high-quality trees of sufficient value to justify the cost of their development.

In order to assure that sufficient material will remain for future selection and breeding work, it would be wise to establish several gene pool reserves before the best natural populations are eliminated or degraded through extensive cutting or inadequate natural regeneration. Because few provenance tests or other plantations have been established so far, there is currently little danger of contamination from plants of non-native origin, but it could become important if planting of yellow birch becomes a common practice in the future. Gene pool reserves should preferably be large ecological or administrative units. One area, that might be suitable, is the 360 acre (145 ha) hemlock-yellow birch preserve of the Flambeau River State Forest in Wisconsin. This is a designated Scientific Area and thus, should be reasonably well protected. Another suggested reserve would be the 5000 acre (2000 ha) "botanical zone" of the Sylvania Recreation Area in Upper Michigan which also contains much yellow birch. Similar reserves could probably be created in the southern Appalachians, New York, New England, and in several Canadian provinces. All gene pool reserves should be further protected by adequate buffer zones.

RESEARCH NEEDS

From the preceding it is evident that we need much more research to complete our knowledge of yellow birch genetics. Some of the needed research is outlined below.

Variation studies have been too few to provide adequate information about the population structure of the species. Although the rangewide study should continue to provide information about broad geographic variation patterns, it has also brought out the need for further research on regional and local variation in a number of characteristics. The work on Quebec and Appalachian populations has already demonstrated that local variation is extensive in this species. Consequently, more studies of regional and local variation should be undertaken with much more intensive sampling of populations than was possible in the rangewide test. Available provenances and open-pollinated progenies should be used for further investigations of variation in phenology, morphology, growth, selected chemical constituents, and chromosome numbers. Later, additional sampling for biosystematic research may be needed. Basic genecological and similar studies can probably be conducted in the nursery. Selected material from these investigations can be moved into the field for further testing and observation.

Multi-purpose testing of progenies is another high priority field of research. From the few tests underway, it is apparent that much individual tree variation is present in yellow birch. Many more trees, including some that are not superior phenotypes, should be tested to determine how much genetic improvement can be expected from selection for particular characteristics. These tests should also serve as a source from which to obtain heritability estimates of important growth and quality traits that are unknown at present. We also need to establish correlations between juvenile and mature characteristics, be they morphological, physiological, or biochemical.

Components of growth require study. Length, width, and density of the crown, photosynthetic efficiency, distribution of photosynthates to stem or crown, utilization of the growing season, and use of available nutrients and water are some of the individual tree characteristics that affect height and diameter growth. If the contribution of each factor and its genetic control can be determined, it may be possible to breed for the characteristics having the greatest effect on growth. For example, where do we want the increased growth to accumulate? For veneer logs, faster diameter growth is more important than greater tree height. Because size and probably density of the crown have a pronounced effect on diameter growth, perhaps we should strive for trees with a relatively large, dense crown and a short, clear bole.

Seed orchard designs and management practices need to be developed. We do not know the optimum number of seedling families or clones to be included in a seed orchard. We also need to know how the families or clones should be arranged within the orchard to ensure maximum cross-fertilization and optimum spacing. Other questions requiring answers are: At what age can we expect trees in the orchards to flower? How much seed will a tree produce and what is the potential seed yield per acre of orchard?

Few management practices for yellow birch seed orchards have been developed. Before production orchards are established it might be wise to set up pilot orchards in which management techniques can be tested. We need to know how long the orchard should be clean-cultivated, the type and amount of fertilizer to use and when it should be applied, and if, when, and how pruning should be carried out. Other important questions are: Can we ensure yearly seed production through proper fertilization, cultivation, and irrigation? What are the easiest and most economical methods of harvesting the seed? If clonal orchards become desirable, for example in a resistance breeding program, can reliable methods of propagating the species by cuttings be found?

Research outside the field of genetics is urgently needed concerning techniques for establishing and maintaining yellow birch plantations. If we are to utilize efficiently the genetically improved seed resulting from improvement programs, we must know how to plant the species and how to take care of the plantations. This knowledge is practically nonexistent at present.

Cytological research is important but of lower priority than the areas just outlined. If, as preliminary work indicates, there is intraspecific variation in the number of chromosomes, the extent and pattern of variation should be investigated. It would also be of interest to determine whether variation in chromosome number is correlated with variation in DNA content. Of more practical importance would be to find out whether the number of chromosomes possessed by a plant is related to its growth rate or other characteristics.

Hybridization research is another low-priority field of study. Although provenance variation in yellow birch appears to be less important than individual tree variation, it would be interesting to produce interprovenance hybrids and compare their growth rate and reaction range with those of other intraspecific hybrids or open-pollinated families. Hybridization of superior or other selected trees would be another fruitful area of research. In addition to providing information about cross-compatibility of the trees, much valuable full-sib material would be produced and would be available for further study. Species hybridization may not lead to much practical improvement, but this type of research should be continued because it can yield much basic information about the phylogeny of the genus and the evolution of the individual species. In order to test the hypothesis of *Betula* phylogeny presented previously, it will be necessary to establish good collections of exotic birches, especially those from China and northeastern Asia that are poorly represented in most western arboreta and botanical gardens.

Studies of isoenzymes and other constituents may help us understand the population structure of yellow birch and could lead to new, simplified breeding methods. These and other basic studies would help elucidate such problems and processes as hybridization, incompatibility, pest resistance, heterosis and inheritance patterns.

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The taxonomy, evolution, migrational history, and distribution of yellow birch (*Betula alleghaniensis* Britt.) are reviewed. Other topics included are reproductive development, compatibility, crossability, controlled pollination, seed handling, and propagation techniques. Variation observed in natural stands, among provenances and among open-pollinated progenies appears random for most characteristics. Clinal variation is rare. Interspecific hybridization work is summarized. Tree improvement programs and areas in need of research are suggested.

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